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Strategies for genetic transfer of an allele for resistance to Phytophthora megasperma f. sp. glycinea Kuan and Erwin in soybean [Glycine max (L.) Merr.]

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STRATEGIES FOR GENETIC TRANSFER OF AN ALLELE FOR RESISTANCE TO PHYTOPHTHORA MEGASPERMA F. SP. GLYCINEA KUAN AND ERWIN IN SOYBEAN (GLYCINE MAX (L.) MERR.)

Iowa State University PH.D. 1987

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Strategies for genetic transfer of an allele for resistance to *Phytophthora megasperma* f. sp. *glycinea* Kuan and Erwin in soybean [*Glycine max* (L.) Merr.]

by

Verni Kitzmann Wehrmann

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INTRODUCTION

Phytophthora stem and root rot, caused by Phytophthora megasperma Drechs. f. sp. glycinea Kuan and Erwin, is one of the most destructive diseases of soybeans [Glycine max (L.) Merr.] (Athow, 1984). It causes pre- and post-emergence damping-off of seedlings and a root and stem rot that results in wilting and death of plants (Kaufmann and Gerdemann, 1958). The disease may cause yield losses of more than 50% in susceptible soybean cultivars (Sinclair, 1982). Schmitthenner (1985) reported: "approximately 16 million acres are now infested with Phytophthora in the United States and Canada".

Shortly after Phytophthora was recognized as a soybean disease, sources of resistance were identified (Suhovecky and Schmitthenner, 1955), and the genetic control of resistance was regarded as monogenic (Bernard et al., 1957). Twenty-five races of Phytophthora and several major genes for resistance have been reported. Backcrossing has been used to transfer major genes for resistance into susceptible cultivars.

Two strategies of backcross have been used in developing soybean cultivars with resistance to Phytophthora. One strategy involves developing homozygous resistant lines and selecting the best line for release as a new cultivar, based on yield tests. The other strategy involves developing homozygous resistant lines, discarding those lines that do not conform

with the phenotype of the recurrent parent, without yield testing. Seeds of uniform lines are composited for release as a new cultivar.

Pugsley (1949) emphasized the need for more precise information on the number of backcrosses necessary to recover the phenotype of the recurrent parent when breeding for disease resistance: "Californian workers have used four to six backcrosses, but experience in South Australia indicates that little is gained by making more than four backcrosses". Wilcox et al. (1971) investigated the number of backcrosses required to transfer a gene for resistance to Phytophthora into susceptible soybean cultivars. They concluded that seven backcrosses are necessary when no selection for agronomic traits is made during backcrossing. However, in recent years most soybean breeders have used less than seven backcrosses for development of Phytophthora-resistant cultivars. No studies have been conducted to verify the results of Wilcox et al. (1971), or to explore the possibility of recovering the yield of the recurrent parent at earlier generations of backcrossing.

The objectives of this study were 1) to determine the number of backcrosses required to transfer a major gene for resistance to Phytophthora into a susceptible cultivar and obtain individual resistant lines with the yield potential of the recurrent parent, and 2) to determine the backcross generation in which a composite of phenotypicaly similar lines will provide the same yield as that of the recurrent parent.

LITERATURE REVIEW

Phytophthora was first detected in soybean in northeastern Indiana in 1948 and in northwestern Ohio in 1951 (Hartwig, 1975). Since that time, the disease has been recognized in several soybean growing areas in the United States (Skotland, 1955; Morgan et al., 1966; Vest et al., 1969; Tachibana et al., 1975).

Herr (1957) described the disease causal organism of phytophthora stem and root rot as *Phytophthora cactorum*. Kaufmann and Gerdemann (1958) proposed the name of the pathogen as *Phytophthora sojae*. Hildebrand (1959) classified the pathogen as *Phytophthora megasperma* Drechs. var. *sojae*. The current identification of the pathogen is *Phytophthora megasperma* Drechs. f. sp. *glycinea* Kuan and Erwin (Kuan and Erwin, 1980).

Phytophthora has been detected in a variety of soil types, especially in poorly drained, clay soils (Schmitthenner, 1963; Brown and Kennedy, 1965; Kittle and Gray, 1979; Sinclair, 1982). Symptoms of infection in susceptible plants are yellowing of the lower leaves, then yellowing of the entire plant, followed by wilting and death (Brown and Kennedy, 1965). Soybean plants resistant to *Phytophthora* produce a phytoalexin toxic to the pathogen (Klarman and Gerdemann, 1963). The inability of plants to produce this substance when inoculated with *Phytophthora* is responsible for susceptibility.

Physiologic Races of *Phytophthora megasperma*

Averre and Athow (1964) noticed differential pathogenicity of *Phytophthora* isolates on soybean. Morgan and Hartwig (1965) grouped isolates of the pathogen into two physiologic races (race 1 and race 2), based on their pathogenicity to specific soybean genotypes. Since that time, 25 physiologic races have been reported. Race 3 was identified by Schmitthenner (1972), race 4 by Schwenk and Sim (1974), races 5 and 6 by Haas and Buzzell (1976), races 7 to 9 by Laviolette and Athow (1977), races 10 to 16 by Keeling (1980), races 17 to 20 by Keeling (1982), races 21 and 22 by Laviolette and Athow (1983), race 23 by White et al. (1983), race 24 by Keeling (1984), and race 25 by Layton et al. (1986). Scientists believe that new races will continue to be found (Walker, 1984).

Inheritance of Resistance to *Phytophthora megasperma*

The genetic control of resistance to *Phytophthora* in soybean has been studied by several authors. Bernard et al. (1957) found that resistance to the disease was controlled by a single dominant gene *Ps*, based on inoculation of progenies from crosses between resistant and susceptible cultivars. The designation for the gene was later changed to *Rps* by Hartwig et al. (1968) to conform to a system of identifying alleles for disease reaction in soybean. Hartwig et al. (1968) indicated that resistance to race 2 was controlled by the allele rps_2, which was part of an allelomorphic series. *Rps* was dominant to

rps$_2$, which was dominant to *rps*. Further inheritance studies confirmed the monogenic control of resistance to *Phytophthora* (Lam-Sanchez et al., 1968).

As new races of the pathogen were identified, genes that provided resistance to specific races were found. Kilen et al. (1974) identified a dominant allele *Rps*$_2$, and indicated that *Rps*$_2$ was at a different locus than the *Rps*, *rps*$_2$, *rps* locus. They suggested changing the previous allele designation *Rps*, *rps*$_2$, and *rps* to *Rps*, *rps*$_1{}^2$, and *rps*$_1$, in order to distinguish it from the second locus. Mueller et al. (1978) identified the allele *Rps*^{c} and suggested changing the *rps*$_1{}^2$ designation to *Rps*^{b}, forming the allelomorphic series *Rps*^{a}, *Rps*^{b}, *Rps*^{c}, and *rps*. They also reported the presence of a dominant allele, *Rps*$_3$, at a different locus from those previously reported.

Laviolette et al. (1979) evaluated the reaction of nine soybean crosses to races 5, 6, 7, 8, and 9. The allele *Rps*^{a} was susceptible to all races tested. The allele *Rps*^{b} showed resistance to all races. The allele *Rps*^{c} gave susceptibility to race 5 and resistance to races 6, 7, 8, and 9. They also reported that these three alleles are located at the same locus. Athow et al. (1980) reported the presence of an allele at a new locus, designated as Rps$_4$, which governs resistance to races 1 to 4. The allele *Rps*$_5$, conferring resistance to races 1 to 5, 8, and 9, was identified by Buzzell and Anderson (1981). They indicated that *Rps*$_5$ could be at the *Rps*$_2$ locus, and that there was no proof that *Rps*$_3$ and *Rps*$_4$ were not at the *Rps*$_2$ locus.

Bernard and Cremeens (1981) identified the allele $\underline{Rps_1}^k$. Schmitthenner (1985) indicated that the allele $\underline{Rps_1}^k$ controls all races from 1 to 24, except races 12, 16, 19, and 20. Layton et al. (1986) reported that $\underline{Rps_1}^k$ is susceptible to race 25. The allele $\underline{Rps_6}$ was identified by Athow and Laviolette (1982). $\underline{Rps_6}$ is similar to $\underline{Rps_4}$, except that it conditions susceptibility to race 13, whereas Rps_4 conditions resistance to the race. Kilen (1986) determined the relationship between $\underline{Rps_2}$, $\underline{Rps_4}$, $\underline{Rps_5}$, and $\underline{Rps_6}$. $\underline{Rps_4}$, $\underline{Rps_5}$, and $\underline{Rps_6}$ are nonallelic to $\underline{Rps_2}$. Athow and Laviolette [unpublished, cited by Athow (1984)] identified the allele $\underline{Rps_7}$, which confers resistance to races 1 to 9, except race 6. The reactions of resistance genes to all known races of *Phytophthora*, except races 6 and 11, are listed in Table 1.

Available evidences indicate that resistance to *Phytophthora* also can be governed by quantitatively inherited genes. Smith and Schmitthenner (1959) reported the presence of modifiers that partially inhibit the action of the major gene for resistance to *Phytophthora*. It was noticed in the early 1970s that acceptable yields could be obtained by growing soybean without specific resistance to *Phytophthora* race 3 in soils infected with race 3 (Schmitthenner, 1985). Anderson (1986) defined as tolerants the plants that support the infection of the pathogen without showing severe symptoms. Cultivars differ in their level of tolerance to *Phytophthora* (Tooley and Grau, 1982). Transgressive segregation for lower and higher levels of tolerance has occurred, and continuous variation for tolerance exists in

Table 1. Reactions of soybean cultivars with their corresponding genes for resistance to physiologic races of *Phytophthora megasperma* Drechs. f. sp. *glycinea* Kuan and Erwin (Adapted from Kilen, 1985)

Source	Gene	Reaction to physiologic race										
		1	2	3	4	5	7	8	9	10	12	13
Harosoy	*rps*	S	S	S	S	S	S	S	S	S	R	S
Mukden	Rps_1	R	R	S	S	S	S	S	S	R	R	R
Sanga	Rps_1[b]	R	S	R	R	R	R	R	R	S	S	R
Mack	Rps_1[c]	R	R	R	S	S	R	R	R	R	S	R
PI 103091[b]	Rps_1[d]	R	R	R	R	R	R	S	R	R	S	R
Kingwa	Rps_1[k]	R	R	R	R	R	R	R	R	R	S	R
CNS	Rps_2	R	R	R	R	-	S	S	R	R	R	R
PI 171442	Rps_3	R	R	R	R	R	S	R	R	S	S	R
PI 172901[b]	Rps_3[b]	R	R	R	R	R	R	-	R	R	R	-
PI 340046[b]	Rps_3[c]	R	R	R	R	S	S	-	S	-	R	-
PI 82312N[b]	Rps_3[d]	R	R	R	R	R	S	-	R	-	-	-
PI 273483D[b]	Rps_3[e]	R	R	R	R	S	S	-	S	-	R	-
PI 86050	Rps_4	R	R	R	R	S	S	S	S	R	R	R
T240	Rps_5	R	R	R	R	R	S	R	R	S	S	R
Altona	Rps_6	R	R	R	R	S	S	S	S	R	R	S
PI 82312N[b]	Rps_7	R	R	R	R	R	R	R	R	-	-	-

[a]Race 25 was proposed by Layton et al. (1986).

[b]Gene symbols not published.

14	15	16	17	18	19	20	21	22	23	24	25[a]
S	S	R	S	R	R	S	S	S	S	S	-
S	R	R	R	R	R	S	S	S	S	R	S
R	R	S	S	R	S	S	R	R	S	S	S
S	R	S	R	S	S	S	R	S	R	R	S
R	R	R	S	R	S	R	R	R	R	R	-
R	R	S	R	R	S	S	R	R	-	-	S
R	S	S	S	-	-	-	-	-	-	-	-
R	S	R	S	R	S	S	S	S	R	S	R
-	-	R	-	-	-	-	-	-	-	-	-
-	-	R	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-
R	-	R	-	-	-	-	-	-	-	-	-
R	R	R	R	R	R	R	R	S	-	-	R
R	S	R	S	S	S	-	S	-	-	-	R
R	R	R	S	R	R	R	R	S	S	S	R
-	-	-	-	-	-	-	-	-	-	-	-

populations (Walker, 1984). Walker and Schmitthenner (1984b) obtained significant improvement of tolerance to Phytophthora through three cycles of recurrent selection with evaluation of S_1 lines. Buzzell and Anderson (1982) and Walker and Schmitthenner (1984a) obtained heritability estimates for tolerance to Phytophthora ranging from 68 to 96% on an entry-mean basis. Walker and Schmitthenner (1984a) emphasized that lines carrying major gene resistance had a higher mean tolerance than lines that did not carry genes for race-specific resistance. This suggested that major gene resistance and tolerance were not completely independent.

Sources of Alleles for Resistance to *Phytophthora megasperma* in Soybean

Soon after Phytophthora was recognized in soybean, resistant cultivars were identified. The cultivars Monroe and Blackhawk were found to be resistant to Phytophthora in field tests as early as 1955 (Suhovecky and Schmitthenner, 1955).

Bernard et al. (1957) identified the Ps allele, later changed to Rps, in the cultivars A.K., Arksoy, Blackhawk, CNS, Dorman, Harly, Illini, Monroe, and Mukden. The allele Rps_2 was found in the cultivar CNS (Kilen et al., 1974). Mueller et al. (1978) identified the allele $Rps_1{}^c$ in PI 54615-1, and Rps_3 in PI 86972-1. Laviolette et al. (1979) identified the allele Rps^a in the cultivar Mukden, Rps^b in PI 84637, and Rps^c in PI 54615-1. The allele Rps_4 was found in PI 86050 (Athow et al., 1980), $Rps_1{}^k$ in the cultivar Kingwa

(Bernard and Cremeens, 1981), $\underline{Rps_5}$ in the experimental line L62-904 (Buzzell and Anderson, 1981), $\underline{Rps_6}$ in the cultivar Altona (Athow and Laviolette, 1982), and $\underline{Rps_7}$ in PI 82312N [Athow and Laviolette, unpublished, cited by Athow (1984)].

Genes for resistance to Phytophthora are present in a large proportion of the available soybean cultivars. More than 40% of the strains in the germplasm collection of Maturity Group V and later are resistant to Phytophthora (Hartwig, 1973). Athow et al. (1974) investigated the reaction of 266 soybean germplasm strains to the Phytophthora races 1, 2, 3, and 4. Various combinations of resistance to those four races were found among the strains. Ninety-five strains were resistant to all four races. Moots et al. (1983) screened 85 soybean cultivars to 14 races of Phytophthora and found 37 cultivars with resistance to one or more races.

Use of the Backcross Method in Plant Breeding

The backcross method was proposed by Harlan and Pope (1922) as a method of incorporating simply inherited traits into an existing cultivar that has a large number of desirable characteristics. The method has been used successfully to transfer genes controlling both quantitatively (Briggs and Allard, 1953; Duvick, 1974) and qualitatively inherited characters (Briggs, 1930; Briggs, 1935; Briggs, 1938; Suneson et al., 1941; Suneson, 1947).

Strategies may vary according to the genetic control of the

trait being transferred. Quantitatively inherited traits, like protein percentage in soybean, may be most effectively transferred by conducting selfing and selection for the trait between backcross generations. Qualitatively inherited traits may be more rapidly incorporated by successive backcrosses to the recurrent parent.

Briggs and Allard (1953) described three important criteria for a successful backcrossing program: 1) the availability of a satisfactory recurrent parent, 2) the retention of a worthwhile intensity of the character being transferred through several backcrosses, and 3) the reconstitution of the phenotype of the recurrent parent by a reasonable number of backcrosses carried out with a population of manageable size. Singh (1975) emphasized that the backcross method has been used in soybean breeding in three different ways: 1) to improve the genetic background of crosses by making one or more backcrosses with the better adapted parent before starting selection for desirable recombinants, 2) to incorporate resistance to diseases and nematodes into otherwise susceptible, high yielding cultivars, and 3) to develop near-isogenic lines for use in inheritance and agronomic studies.

Systems of Designation of Backcross Derivatives

Johnson and Unrau (1950) described a system of backcross designations that allows the reader to identify the recurrent parent, the number of backcrosses, interruptions of backcrossing

by selfing, resumption of backcrossing after selfing, and so forth. For example, the cross A x B, with three backcrosses to B, followed by two selfing generations and one more backcross to B would be designated A x $B_{4(2)1}$. The number 4, after B, refers to the three initial backcrosses and represents four doses of B in that cross. The number 2 represents the two selfing generations, and 1 represents one backcross after the selfing generations. Breeders commonly describe the parentage of backcross derived germplasm with a number designating the doses of the recurrent parent, such as A x B^4, which represents three backcrosses to B. Soybean cultivars developed by backcrossing have been designated by the name of the recurrent parent and the year that the backcross derivative was released as a cultivar: Hawkeye 63 (Bernard, 1964), Amsoy 71 (Probst et al., 1972), Beeson 80 (Wilcox et al., 1980), Vinton 81 (Fehr et al., 1984), and Century 84 (Walker et al., 1986).

Number of Backcrosses Required to Recover the Phenotype of the Recurrent Parent

The recovery of the phenotype of the recurrent parent is primarily a function of the number of backcrosses. The number of backcrosses is chiefly dependent on the agronomic performance of the donor parent and on the decision of whether or not to carry out selection during backcrossing. Early reports on the use of backcrossing in plant breeding tended to indicate that a large number of backcrosses was necessary to recover the phenotype, especially yield, of the recurrent parent. The use of

agronomically poor donor parents may have been the reason for such a recommendation.

Selection for the phenotype of the recurrent parent in the early backcross generations is effective in hastening the recovery of the characteristics of the recurrent parent (Briggs and Allard, 1953). Briggs and Allard (1953) stated: "It is believed that selection for the type of the recurrent parent, if based on moderate-sized populations, is equivalent to one or two additional backcrosses in a continuous series". They noted, however, that after the third backcross, the population resembles the recurrent parent so closely that further selection is largely ineffective, and the yielding ability of that generation has not yet equaled that of the recurrent parent. They justified such results with the theoretical considerations of Riddle and Baker (1944): "...if the parents differ in 21 gene pairs, after six backcrosses 95.8% of the population will be genetically identical to the recurrent parent or differ from it by a single allele. After three backcrosses and the same number of gene differences, only 24% of the population would meet such classification". Further, Briggs and Allard (1953) stated: "Six backcrosses, when coupled with rigid selection in the early generations, have proved satisfactory in a large number of backcross programs... as many as 10 backcrosses have been made when population sizes were small and little or no selection was practiced".

Use of the Backcross Method for Transferring a Specific Gene for Resistance to *Phytophthora megasperma* in Soybean

Most of the soybean cultivars grown in the Midwest at the time *Phytophthora* was recognized were susceptible to the pathogen (Schmitthenner, 1963). Because only one pair of major genes was considered to be involved, it was possible to transfer resistance to improved cultivars readily through a backcross program. The first soybean cultivars developed in the United States by the backcross method were resistant versions of cultivars susceptible to *Phytophthora* (Anonymous, 1963).

Wilcox et al. (1971) indicated that the development of soybean cultivars resistant to *Phytophthora* meet the criteria listed by Briggs and Allard (1953) for a successful backcrossing program. They investigated the use of backcross for transferring resistance to *Phytophthora* from the soybean cultivar Mukden into five cultivars or experimental lines. Seven backcrosses were made using a random resistant plant to cross with the recurrent parent in each generation. Two resistant and two susceptible lines were derived from each of two heterozygous plants of each backcross generation and evaluated for agronomic traits. The study revealed varied results among crosses. However, the recovery of the recurrent parent phenotype was generally slower than predicted if only additive genetic control was assumed for the agronomic traits. The susceptible lines tended to outyield the resistant ones. However, they did

find a resistant line that significantly outyielded the susceptible lines of that generation. They concluded that seven backcrosses without selection for agronomic traits, followed by the elimination of progeny rows that did not visually conform to the phenotype of the recurrent parent would be the most efficient way to add Phytophthora resistance to susceptible cultivars or experimental lines.

Resistance to Phytophthora has been incorporated into several soybean cultivars. This process generally involved fewer than seven backcrosses. Of the 20 soybean cultivars developed and released from 1963 to 1986, only six cultivars were developed using seven backcrosses. The remaining 14 cultivars involved six or fewer backcrosses (Table 2).

Associations Between Resistance to Phytophthora and Other Agronomic Traits of Soybean

Backcross-derived cultivars with resistance to Phytophthora have frequently yielded less than their susceptible recurrent parents in the absence of the disease. In the 1964 Uniform Soybean Yield Test of the North Central States, the susceptible cultivars Harosoy, Hawkeye, and Lindarin each yielded about one bushel per acre more than their respective resistant backcross-derivatives Harosoy 63, Hawkeye 63, and Lindarin 63 (Cartter, 1965).

Studies were conducted to investigate the possible effects of alleles for resistance to Phytophthora on yield and other plant characteristics. Some of the reported results are

Table 2. List of the soybean cultivars developed by backcrossing resistance to *Phytophthora* into susceptible cultivars

Cultivar	Number of Backcrosses	Pedigree	Reference
Hardin	2	Corsoy x Cutler 71	Fehr et al. (1983)
Cutler 71	3	Cutler x (Kent-Rpsr x p-SL-5)	Probst et al. (1971)
Lindarin 63	4	Lindarin x Mukden	Probst et al. (1964)
Vickery	4	Corsoy x (L65-1342 x Mack & Anoka x Mack)	Fehr et al. (1981)
Vinton 81	4	L60-347-4-4G-2B x Vinton	Fehr et al. (1984)
Union	4	Williams x SL12	Bernard and Cremeens (1982)
Century 84	4	Century x Williams 82	Walker et al. (1986)
Clark 63	a) 4 b) 6	(Clark x S54-1714) (Clark x Blackhawk)	Williams and Bernard (1964)
Lee 68	5	Lee x Arksoy	Caviness and Walters (1968)
Hawkeye 63	6	Hawkeye x Blackhawk	Bernard (1964)
Keller	6	Beeson 80 x PRX9-29	Athow et al. (1984a)

Miami	6	Wells II x PRX9-274	Athow et al. (1984b)
Winchester	6	Williams x PRX12-112	Athow et al. (1984c)
Hogdson 78	6	Hogdson x Merit	Lambert and Kennedy (1979)
Harosoy 63	7	Harosoy x Blackhawk	Bernard (1964)
Chippewa 64	7	Chippewa x Blackhawk	Bernard (1964)
Amsoy 71	7	Amsoy x C1253	Probst et al. (1972)
Hood 75	7	Hood x Arksoy	Caviness and Walters (1976)
Wells II	7	Wells x Arksoy	Wilcox et al. (1979)
Beeson 80	7	Beeson x Arksoy	Wilcox et al. (1980)

conflicting. Haque (1964) obtained evidences for linkage in the coupling phase between the allele Ps for resistance to Phytophthora, later changed to Rps, and the allele for lateness in maturity. Kilen and Barrantine (1963) reported that the Rps_1 locus is 7 map units (recombination percentage of 7%) from the Hm locus controlling sensitivity to metribuzin. Cooper and Waranyuwat (1985) compared the effect of the Pd allele for dense pubescence and the Rps_1^a allele for resistance to Phytophthora in near-isogenic lines. Addition of Pd and Rps_1^a to indeterminate near-isogenic lines increased plant height and lodging, but decreased yield. In the determinate near-isogenic lines with Pd and Rps_1^a, where no lodging occurred, plant height was increased and yields were either increased or there was no difference in yield. They suggested that the failure of the Pd and Rps_1^a alleles to increase yield and their occasional association with decreased yield was due to the increased lodging associated with increased vegetative growth.

Singh and Lambert (1985) investigated the effect of the Rps_1 allele for resistance to Phytophthora on several agronomic traits. Closely related lines with and without Rps_1 were evaluated in disease-free environments. Resistant and susceptible lines were not significantly different in yield, maturity, lodging, plant height, seed quality, seed size, protein percentage, or oil percentage. They emphasized that there was no convincing evidence of any genetic association between the Rps_1 allele and any of the traits studied.

MATERIAL AND METHODS

The experimental material used in this study was developed by transferring the allele $\underline{Rps_1}^k$ for resistance to *Phytophthora megasperma* Drechs. f. sp. *glycinea* Kuan and Erwin from the cultivar Williams 82 into the susceptible cultivar Cumberland and the experimental line A78-123018. Cumberland was selected for its high yield, desirable agronomic characteristics and suitable maturity for southern Iowa. In the 1980 Uniform Soybean Tests, Northern States, Cumberland yielded 6% more than Williams 82. A78-123018 was selected for its high yield and suitable maturity for northern Iowa. Based on a three-year mean from 1980 to 1982, A78-123018 ranked first among the group I genotypes tested in the Uniform Soybean Tests, Northern States. Williams 82 was chosen as the donor of the gene $\underline{Rps_1}^k$, which confers specific resistance to many races of *Phytophthora* (Kilen, 1985). The performance of the parents is presented in Table 3.

The development of the experimental material of the A78-123018 and Cumberland populations is outlined in Figures 1 to 5. Single crosses were made of A78-123018 x Williams 82 and Cumberland x Williams 82 at the Isabela Substation, University of Puerto Rico in January, 1981. Six hybrid seeds of each cross were obtained. At Ames in 1981, seven BC_1F_1 seeds were produced by backcrossing the F_1 plants to each of the recurrent parents. Cumberland and A78-123018 were used as male

Table 3. Mean values for agronomic traits of A78-123018, Cumberland, and Williams 82

Parent	Trait	
	Yield	Maturity
	bu/acre	date
Recurrent parents		
A78-123018[a]	47.9	Sept. 17
Cumberland[b]	45.7	Sept. 23
Donor parent		
Williams 82[b]	43.3	Sept. 25

[a]Source: U.S. Dept. of Agriculture, 1982. Uniform Soybean Test for Northern States. Mean of 1980, 1981 and 1982.

[b]Source: U.S. Dept. of Agriculture, 1980. Uniform Soybean Test for Northern States.

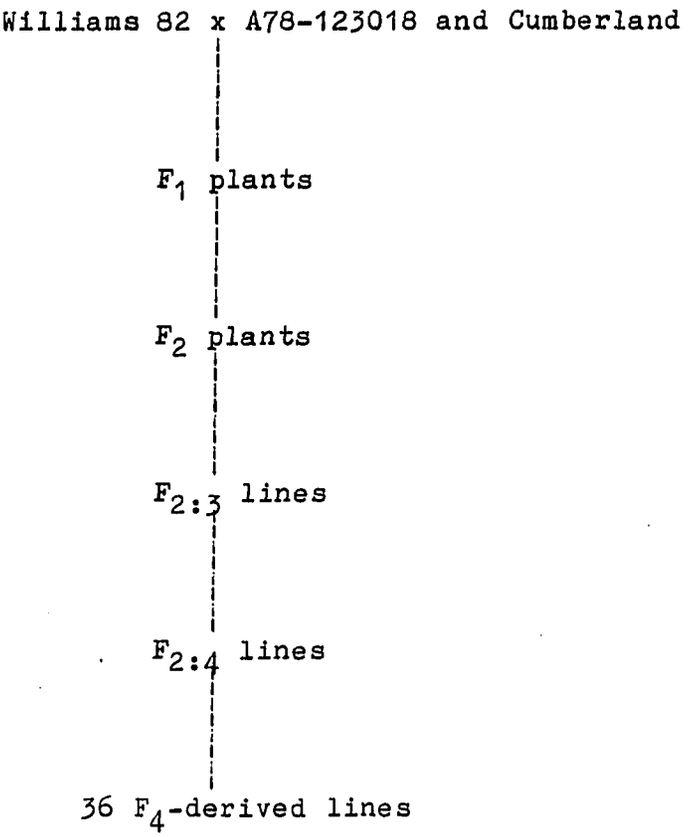

Fig. 1. Outline of the development of the experimental material for the BC_0 generation of the A78-123018 and Cumberland populations

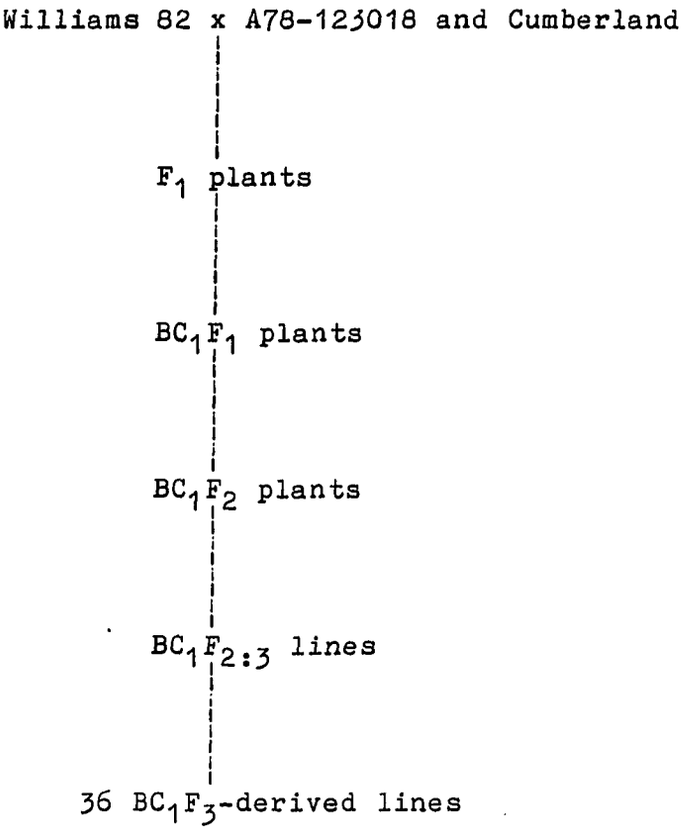

Fig. 2. Outline of the development of the experimental material for the BC_1 generation of the A78-123018 and Cumberland populations

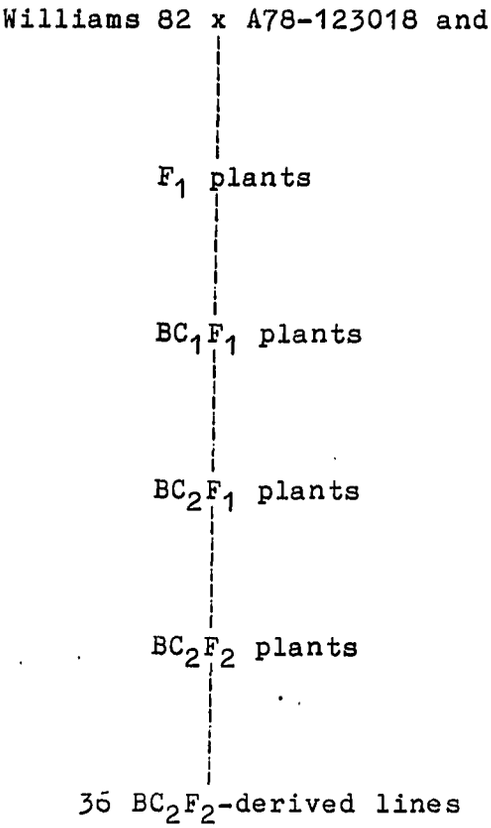

Fig. 3. Outline of the development of the experimental material for the BC_2 generation of the A78-123018 and Cumberland populations

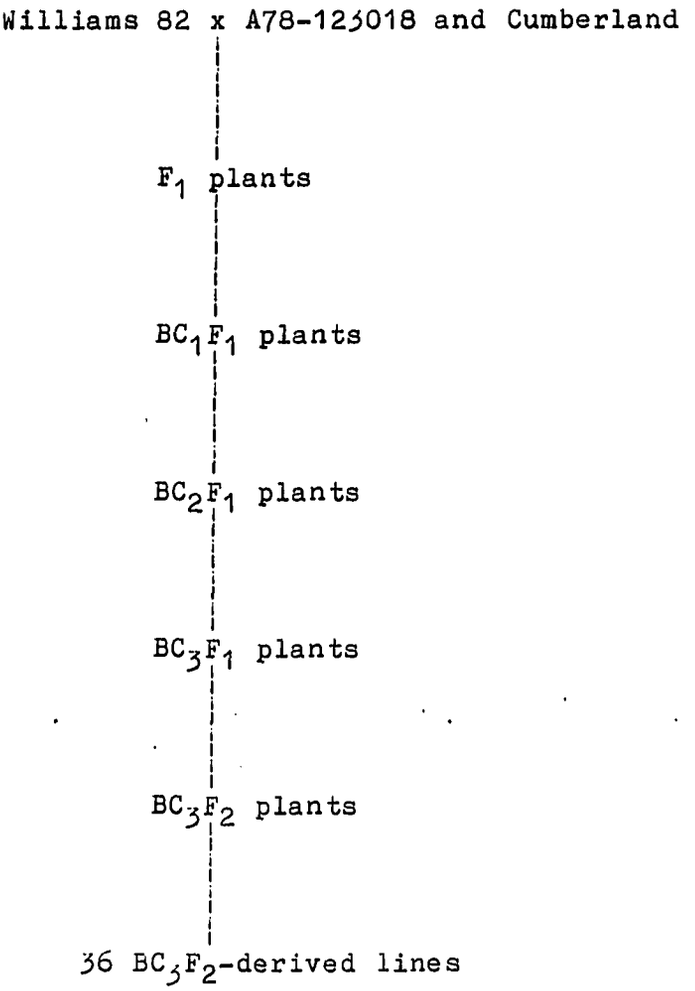

Fig. 4. Outline of the development of the experimental material for the BC_3 generation of the A78-123018 and Cumberland populations

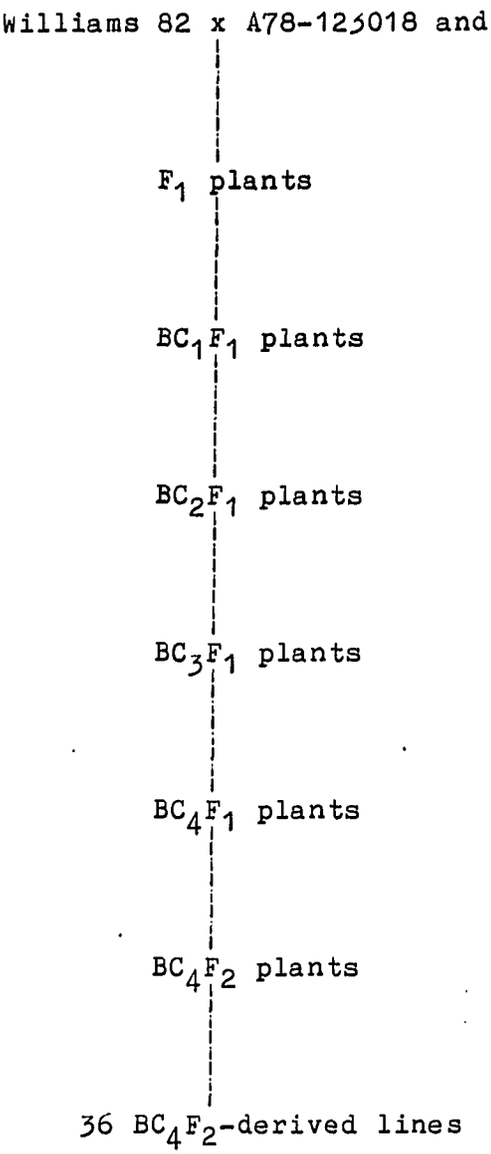

Fig. 5. Outline of the development of the experimental material for the BC_4 generation of the A78-123018 and Cumberland populations

parents for this and all succeeding backcrosses. In Puerto Rico during November of 1981, seven BC_2F_1 seeds were obtained from each of the Cumberland and A78-123018 BC_1F_1 plants. Twenty BC_1F_2 seeds of every BC_1F_1 plant used for crossing were sent to Ames for progeny testing for Phytophthora resistance. In Puerto Rico during February 1982, seven BC_3F_1 seeds were obtained from those BC_2F_1 plants that traced to resistant BC_1F_2 progenies. BC_2F_2 seeds also were harvested from each BC_2F_1 plant.

The fourth backcross was made at Ames in 1982. BC_3F_1 seeds were planted. BC_2F_1 plants used for crossing in the previous season were progeny tested for resistance to Phytophthora. BC_3F_1 plants that traced to a heterozygous resistant BC_2F_1 plant were used for crossing. Ten BC_4F_1 seeds were obtained from each of 13 BC_3F_1 plants of each population. During the same season, a program was initiated to obtain lines homozygous for Phytophthora resistance. F_2 and BC_1F_2 plants were grown at Ames and each plant was harvested individually. BC_2F_2 plants were grown in Puerto Rico and each plant was harvested individually. In Puerto Rico during November 1982, $F_{2:3}$ lines were grown and F_4 seeds were harvested from each line. During the same season BC_4F_2 seeds were harvested from BC_4F_1 plants. In Puerto Rico during February 1983, $F_{2:4}$ lines, $BC_1F_{2:3}$ lines, BC_3F_2 plants, and BC_4F_2 plants were grown and each plant was harvested individually.

$F_{4:5}$, $BC_1F_{3:4}$, $BC_2F_{2:3}$, $BC_3F_{2:3}$, and $BC_4F_{2:3}$ lines were grown at Ames in 1983. For the BC_4 generation, 164 lines of the

A78-123018 population and 153 lines of the Cumberland population were planted in one set of 320 entries using one replication in one location. The entries were planted in rows 75 cm long with 20 seeds per row. Maturity checks were planted as a border on both sides of each set. In each population, 250 plants were harvested from rows segregating for resistance to Phytophthora. The plants had a maturity within 3 days of that of the recurrent parent and were phenotypically similar to their recurrent parent. For each of the BC_0, BC_1, BC_2, and BC_3 generations of both populations, a set of 110 entries was planted. Each set contained 10 replications of the recurrent parent. They were planted in single-hill plots spaced 1 x 1 m with 12 seeds per plot. Ten seeds of each entry were saved for Phytophthora screening to determine the presence of the Rps_1^k allele. The Phytophthora screening test was conducted in the greenhouse. Lines that were phenotypically similar to the recurrent parent in the field, and homozygous for the Rps_1^k allele were selected. The procedure for determining the presence of the Rps_1^k allele is described below.

Ten seeds from each line were planted in 10 cm clay pots in the greenhouse. The cultivars Clark (susceptible), Clark 63 (resistant), and BSR 201 (resistant) were planted as checks to determine the effectiveness of the test. Eight days after planting, the plantlets were inoculated with mycelia of the pathogen from a culture medium. Inoculation was done by cutting a 1 cm slit in the stem below the cotyledonary node.

A small piece of mycelia was inserted into the slit of the stem. Four days after inoculation, the plantlets were scored for symptoms of Phytophthora. Scores were recorded according to the formula: Disease score = No. of plants infected/Total number of plants in a pot. A plant was considered infected when rotted beyond the point of inoculation.

The genetic constitution of the lines was determined according to the following criteria: when none or one plant in a pot was infected, the line was considered homozygous for the Rps_1^k allele; when two to eight plants were infected, the line was considered heterozygous for the Rps_1^k allele; and when nine or more plants were infected, the line was considered homozygous for the rps_1^k allele. Fifty lines from each backcross generation were harvested in the field, based on the following criteria: 1) homozygous resistant to the disease based on the greenhouse screening; 2) maturity within 3 days of the maturity of the recurrent parent; and 3) desirable agronomic characteristics. At Ames in the winter of 1983, the BC_4F_2-derived lines were screened for Phytophthora resistance using race 1 of the pathogen. Fifty BC_4F_2-derived lines homozygous for the Rps_1^k allele were selected.

Fifty lines of each backcross generation were grown in Iowa during the summer of 1984. Twelve seeds per entry were planted in single-hill plots spaced 1 m apart. Thirty-six lines per backcross generation were randomly selected to be used as the experimental material for the present study.

Evaluation of Individual Lines

The 36 lines of each backcross generation were planted in two replications of a randomized complete-block design at Ames in 1985. Lines were grouped in four sets of 50 entries each. Each set contained 9 lines of each backcross generation, three replications of the recurrent parent and two check cultivars. In the Cumberland population, one of the check cultivars was the donor parent. The same experiment was planted again in 1986 at two Iowa locations. The A78-123018 population was planted at Ames and Spencer and the Cumberland population at Stuart and Ottumwa.

In both years, the plots were two rows 5 m long with 70 cm between rows within a plot and 1 m between rows of adjacent plots. The planting rate was 27 seeds per meter of row. The plots were end-trimmed to 3 m before harvest. The seed yield, lodging score and plant height were determined for each plot at each environment. Maturity date was determined at Ames in 1985 for both populations, at Ames in 1986 for the A78-123018 population, and at Stuart in 1986 for the Cumberland population.

Evaluation of Bulks of Lines

In this study, the performance of a backcross generation was estimated in two ways. One way was by averaging the performance of the individual lines of a backcross generation. The other was by bulking a sample of 14 seeds from each line of each backcross generation, and evaluating the performance of the

bulks.

The bulks were planted in two replications of a randomized complete-block design at three Iowa locations in 1985 and 1986. They were grouped into sets of 10 entries each. In 1985, each set of the A78-123018 population contained a bulk of each backcross generation and five check cultivars, while in the Cumberland population each set contained a bulk of each backcross generation, the donor parent, and four check cultivars. In 1986, three of the five check cultivars were replaced by the recurrent parent in the A78-123018 population, and three of the four check cultivars were replaced by the recurrent parent in the Cumberland population. Bulks of the A78-123018 population were planted at Ames, Manson, and Corwith in 1985, and at Ames, Spencer, and Corwith in 1986. Bulks of the Cumberland population were planted at Ames, Stuart and Ottumwa in both years.

Plots were four rows 5 m long with 70 cm between rows. The planting rate was 25 seeds per meter of row. The two center rows of each plot were end-trimmed to 3 m before harvest. The seed yield, lodging score and plant height were determined for the two center rows of each plot at each environment. Maturity date was determined at Ames and Corwith for the A78-123018 population, and at Ames and Stuart for the Cumberland population.

Character Measurements

Seed yield was measured as the weight of the harvested sample that had been dried artificially at 40 C for 2 days before

weighing, and was expressed in grams per meter square. Maturity date was determined as the number of days after August 31, when 95% of the pods had reached their mature color. Plant height was determined at maturity as the distance from the soil surface to the terminal node with a pod on the main stem. Lodging score was rated at maturity on a scale of 1 to 5, with 1 representing all plants erect and 5 all plants prostrate.

Statistical Analyses

Analyses of variance were performed for all traits at individual environments and combined across environments. In the experiments with the individual lines, lines and environments were assumed to be random effects, whereas sets and backcross generations were considered to be fixed effects. In the experiments with the bulks, environments were assumed to be random effects and entries were considered to be a fixed effect. To assess the significance of the genetic variance among lines and genetic effects among backcross generations, the check cultivars were not included in the analyses.

Data of the experiment with individual lines were analyzed at individual environments according to the model:

$$Y_{ijkl} = u + S_i + R_{ij} + G_{il} + L_{ilk} + e_{ijlk}$$

where: Y_{ijkl} = observed value of the k^{th} line from the l^{th} backcross generation within the i^{th} set in the j^{th} replication.

u = overall mean

$i = 1$ to 4

$j = 1$ to 2

$k = 1$ to 9

$l = 1$ to 6, and 1 to 7

S_i = effect of the i^{th} set

R_{ij} = effect of the j^{th} replication within the i^{th} set

G_{il} = effect of the l^{th} backcross generation within the i^{th} set

L_{ilk} = effect of the k^{th} line within the l^{th} backcross generation of the i^{th} set

e_{ijkl} = error associated with the $ijkl^{th}$ observation.

The significance of the backcross generations within sets, replications within sets, and lines within backcross generations within sets effects were tested against the error mean squares. The significance of the sets effect was tested against the (lines within sets) plus (replications within sets) minus (error mean squares).

Data of the experiment with individual lines were combined across environments according to the model:

$$Y_{hijkl} = u + E_h + S_i + R_{ijh} + G_{il} + L_{ilk} + ES_{hi} + EG_{ilh} + EL_{ilkh} + e_{ijklh}$$

where: Y_{ijklh} = observed value of the k^{th} line from the l^{th} backcross generation within the j^{th} replication of the i^{th} set in the h^{th} environment.

u = overall mean

$h = 1$ to 3

$i = 1$ to 4

$j = 1$ to 2

$k = 1$ to 9

$l = 1$ to 6, and 1 to 7

E_h = effect of the h^{th} environment

S_i = effect of the i^{th} set

R_{ijh} = effect of the j^{th} replication within the i^{th} set within the h^{th} environment

G_{il} = effect of the l^{th} generation within the i^{th} set

L_{ilk} = effect of the k^{th} line within the l^{th} generation within the i^{th} set

ES_{ih} = effect of the interaction of the h^{th} environment with the i^{th} set

EG_{ilh} = effect of the interaction of the h^{th} environment with the l^{th} backcross generation within the i^{th} set

EL_{ilkh} = effect of the interaction of the h^{th} environment with the k^{th} line within the l^{th} backcross generation within the i^{th} set

e_{ijklh} = error associated with the $ijklh^{th}$ observation.

The significance of the lines within backcross generations within sets effect was tested against the environments x lines within backcross generations within sets mean squares. The significance of the backcross generations within sets effect was tested against the environments x backcross generations within sets mean squares. The significance of the replications within

sets within environments effect was tested against the error mean squares. The significance of the sets effect was tested against the (replications within sets within environments) plus (lines within sets) plus (environments x sets) minus (environments x lines within sets) minus (error mean squares). The significance of the environments effect was tested against the (replications within sets within environments) plus (environments x sets) plus (environments x lines within sets) minus (twice the error mean squares). The significance of the environments x sets, environments x backcross generations within sets, and environments x lines within backcross generations within sets effects were tested against the error mean squares.

Data of the experiment with the bulks were analyzed at individual environments according to the model:

$$Y_{ij} = u + R_i + E_j + e_{ij}$$

where: Y_{ij} = observed value of the j^{th} entry within the i^{th} replication.

u = overall mean

i = 1 to 2

j = 1 to 5, 1 to 6, and 1 to 7

R_i = effect of the i^{th} replication

E_j = effect of the j^{th} entry

e_{ij} = error associated with the ij^{th} observation.

The effect of entries and replications were tested against the error mean squares.

Data of the experiments with the bulks were combined across

environments according to the model:

$$Y_{ijl} = u + L_i + R_{ij} + E_l + EL_{il} + e_{ijl}$$

where: Y_{ijl} = observed value of the l^{th} entry in the j^{th} replication within the i^{th} environment.

u = overall mean

i = 1 to 6

j = 1 to 2

l = 1 to 5, 1 to 6, and 1 to 7

L_i = effect of the i^{th} environment

R_{ij} = effect of the j^{th} replication within the i^{th} environment

E_l = effect of the l^{th} entry

EL_{il} = effect of the interaction of the i^{th} environment with the l^{th} entry

e_{ijl} = error associated with the ijl^{th} observation.

The effect of entries was tested against the entries x environments mean squares. The effect of environments was tested against the (replications within environments) plus (entries x environments) minus (error mean squares). The effects of the replications within environments and entries x environments were tested against the error mean squares.

The least significant difference (LSD) and the Duncan's New Multiple Range Test were calculated for those traits that had significant mean squares for entries in the analysis of variance. For comparing means of individual lines with the recurrent parent, or of the donor parent with the recurrent parent,

the LSD value was computed using the equation $LSD = t_{df,0.05}\sqrt{EMS(1/n1 + 1/n2)}$, where EMS = error mean squares used for calculating the significance of the lines within sets effect, n1 = number of values used in computing the mean of the recurrent parent, and n2 = number of values used in computing a line mean. For comparing means of individual lines among themselves, the Duncan's New Multiple Range Test was computed using the formula $D = q_{p,df}0.05\sqrt{2EMS/n}$, where EMS = error mean squares for calculating the significance of the lines within sets effect, and n = number of values used in computing a line mean.

For comparing means of backcross generations with the recurrent parent, the LSD value was computed using the equation $LSD = t_{df,0.05}\sqrt{EMS(1/n1 + 1/n2)}$, where EMS = error mean squares used for calculating the significance of the entries effect, n1 = number of values used to compute the mean of the recurrent parent, and n2 = number of values used in computing a line mean. For comparing means of backcross generations among themselves, the Duncan's New Multiple Range Test was computed using the formula $D = q_{p,df}0.05\sqrt{2EMS/n}$, where EMS = error mean squares for calculating the significance of the entries effect, and n = number of values used in computing a backcross generation mean.

Table 4. Form of the analyses of variance for data from the individual lines of the A78-123018 and Cumberland populations combined across environments

Sources of Variation	d.f.[a]	Expected Mean Squares
Environments (E)	(e-1)	$\sigma' + l\sigma'_{r/s/e} + rl\sigma'_{es} + r\sigma'_{el/s} + rls\sigma'_{e}$
Sets (S)	(s-1)	$\sigma' + l\sigma'_{r/s/e} + rlg\sigma'_{es} + rge\sigma'_{l/s} + rleK_{s}$
Replications/S/E	se(r-1)	$\sigma' + l\sigma'_{r/s/e}$
Lines (L)/S	s(l-1)	$\sigma' + r\sigma'_{el/s} + re\sigma'_{l/s}$
Generations (G)/S	s(g-1)	$\sigma' + r\sigma'_{eg/s} + reK_{g/s}$
L/G/S	gs(l-1)	$\sigma' + r\sigma'_{el/g/s} + re\sigma'_{l/g/s}$
$L/BC_0/S$	s(l-1)	$\sigma' + r\sigma'_{el/0/s} + re\sigma'_{l/0/s}$
$L/BC_1/S$	s(l-1)	$\sigma' + r\sigma'_{el/1/s} + re\sigma'_{l/1/s}$
$L/BC_2/S$	s(l-1)	$\sigma' + r\sigma'_{el/2/s} + re\sigma'_{l/2/s}$
$L/BC_3/S$	s(l-1)	$\sigma' + r\sigma'_{el/3/s} + re\sigma'_{l/3/s}$
$L/BC_4/S$	s(l-1)	$\sigma' + r\sigma'_{el/4/s} + re\sigma'_{l/4/s}$

E x S	(e-1)(s-1)	$\sigma' + rl\sigma'_{es}$
E x L/S	(e-1)s(l-1)	$\sigma' + r\sigma'_{el/s}$
E x G/S	(e-1)s(g-1)	$\sigma' + r\sigma'_{eg/s}$
E x L/G/S	(e-1)sg(l-1)	$\sigma' + r\sigma'_{el/g/s}$
E x L/BC_0/S	(e-1)s(l-1)	$\sigma' + r\sigma'_{el/0/s}$
E x L/BC_1/S	(e-1)s(l-1)	$\sigma' + r\sigma'_{el/1/s}$
E x L/BC_2/S	(e-1)s(l-1)	$\sigma' + r\sigma'_{el/2/s}$
E x L/BC_3/S	(e-1)s(l-1)	$\sigma' + r\sigma'_{el/3/s}$
E x L/BC_4/S	(e-1)s(l-1)	$\sigma' + r\sigma'_{el/4/s}$
Error	e(r-1)(l-1)	σ'

[a] e = environments, s = sets, r = replications, and l = lines.

Table 5. Form of the analyses of variance for data from the individual lines of the A78-123018 and Cumberland populations at individual environments

Sources of Variation	df[a]	Expected Mean Squares
Sets (S)	(s-1)	$\sigma' + r\sigma'_{l/s} + l\sigma'_{r/s} + rlK_s$
Replications/S	s(r-1)	$\sigma' + l\sigma'_{r/s}$
Lines (L)/S	s(l-1)	$\sigma' + r\sigma'_{l/s}$
Generations (G)/S	s(g-1)	$\sigma' + rlK_{g/s}$
L/G/S	sg(l-1)	$\sigma' + r\sigma'_{l/g/s}$
$L/BC_0/S$	s(l-1)	$\sigma' + r\sigma'_{l/0/s}$
$L/BC_1/S$	s(l-1)	$\sigma' + r\sigma'_{l/1/s}$
$L/BC_2/S$	s(l-1)	$\sigma' + r\sigma'_{l/2/s}$
$L/BC_3/S$	s(l-1)	$\sigma' + r\sigma'_{l/3/s}$
$L/BC_4/S$	s(l-1)	$\sigma' + r\sigma'_{l/4/s}$
Error	(r-1)(l-1)	σ'

[a] s = sets, r = replications, l = lines, and g = generations.

Table 6. Form of the analyses of variance for data from the bulks of lines from each backcross generation of the A78-123018 and Cumberland populations combined across environments

Sources of Variation	df[a]	Expected Mean Squares
Environments (L)	(l-1)	$\sigma' + le\sigma'_{r/l} + r\sigma'_{le} + re\sigma'_{l}$
Replications/L	l(r-1)	$\sigma' + le\sigma'_{r/l}$
Entries (E)	(e-1)	$\sigma' + r\sigma'_{le} + rlK_e$
E x L	(l-1)(e-1)	$\sigma' + r\sigma'_{le}$
Error	(r-1)l(e-1)	σ'

[a] l = environments, r = replications, and e = entries.

Table 7. Form of the analyses of variance for the data from the bulks of lines from each backcross generation of the A78-123018 and Cumberland populations at individual environments

Sources of Variation	df[a]	Expected Mean Squares
Replications	(r-1)	$\sigma' + l\sigma'_{r}$
Entries	(e-1)	$\sigma' + rK_e$
Error	(r-1)(e-1)	σ'

[a] r = replications, and e = entries.

RESULTS

Combined analyses of variance for the A78-123018 population indicated significant differences among lines within sets for all traits (Table 8). The mean squares of the lines within sets were partitioned into backcross generations within sets and lines within backcross generations within sets. Significant differences among backcross generations within sets and among lines within backcross generations within sets were found for all traits. The mean squares for lines within backcross generations within sets were further subdivided into mean squares for lines within each backcross generation. There was no significant difference for yield among lines within any backcross generation, except within the BC_1 generation. Significant differences were found for all other traits within each backcross generation, except for lodging score within the BC_3 and BC_4 generations and for plant height within the BC_4 generation.

There was no significant difference among sets of the A78-123018 population for any trait. Significant sets x environments interactions were detected for all traits. Significant differences among environments were found for all traits. Significant environments x lines within sets interactions were obtained for all traits, except maturity. The mean squares for environments x lines within sets were partitioned into environments x backcross generations within sets and environments x lines within backcross generations within

Table 8. Analysis of variance for four traits of lines from the A78-123018 population combined across three environments

Sources of Variation	df	Means Squares			df[a]	Mean Squares
		Yield	Lodging	Height		Maturity
Environments (E)	2	854572**	4954.00**	1182**	1	1816.09**
Sets (S)	3	4824	87.15	145	3	29.29
Replications/S/E	12	6484**	50.10**	150**	8	33.47**
Lines (L)/S	180	808**	22.75**	167**	180	12.87**
Generations (G)/S	20	2394**	82.74**	229**	20	13.45**
L/G/S	160	609*	15.25**	159**	160	12.70**
$L/BC_0/S$	32	677	29.15**	386**	32	17.40**
$L/BC_1/S$	32	867*	12.29**	211**	32	17.00**
$L/BC_2/S$	32	395	14.40*	92**	32	12.94**
$L/BC_3/S$	32	343	11.14	72**	32	8.16*
$L/BC_4/S$	32	767	9.28	36	32	8.00**

E x S	6	5350**	15.61**	65*	3	24.93**
E x L/S	360	498**	5.89**	31*	180	2.82
E x G/S	40	578**	6.08	26	20	2.85
E x L/G/S	320	488**	5.86**	31*	160	2.81
E x $L/BC_0/S$	64	461	4.24	40**	32	2.20
E x $L/BC_1/S$	64	470*	4.79	36**	32	2.80
E x $L/BC_2/S$	64	441	7.23**	29	32	1.95
E x $L/BC_3/S$	64	432	7.21**	23	32	4.29**
E x $L/BC_4/S$	64	635**	5.84*	28	32	2.82
Error	588	351	4.41	24	392	2.35
CV (%)		6.4	10.1	5.9		13.3

[a]Data from only two environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

sets. No significant environments x backcross generations interaction was observed, except for yield. Environments x lines within backcross generations within sets interactions were significant for all traits except maturity. The mean squares for environments x lines within backcross generations within sets was further subdivided into environments x lines within each backcross generation. Significant interactions with environments were found for yield in the BC_1 and BC_4 generations and for lodging score in the BC_2, BC_3, and BC_4 generations. No significant interaction with environments was detected for maturity, except in the BC_3 generation, and for plant height, except in the BC_0 and BC_1 generations.

Means combined over environments for the A78-125018 population indicated that the BC_0F_4-derived lines yielded significantly less than the other backcross generations and the recurrent parent (Table 9). There was no difference in yield among the BC_1, BC_2, BC_3, and BC_4 generations and the recurrent parent. All backcross generations were significantly later in maturity than the recurrent parent. BC_3F_2-derived lines were the latest in maturity, followed by the BC_4F_2-derived lines. There was no significant difference in maturity among the other backcross generations. Lodging score of the BC_2 and BC_4 generations was not significantly different from that of the recurrent parent. Lodging score of the BC_0F_4-derived lines was significantly lower than that of the other backcross generations and the recurrent parent. BC_2F_2- and BC_3F_2-derived

Table 9. Means of the population, five backcross generations, and the recurrent parent for four traits of lines from the A78-123018 population combined across three environments

Backcross Generation	Expected[a] Yield	Trait			
		Yield	Maturity[b]	Lodging	Height
	$g\ m^{-2}$	$g\ m^{-2}$	days	score	cm
Population mean		291	11.4	2.1	84
BC_0	282.5	280b[c]	11.1c	1.9d	83b
BC_1	289.2	291a	11.0c	2.0c	83b
BC_2	292.6	292a	11.1c	2.1b	85a
BC_3	294.3	292a	12.0a	2.2a	85a
BC_4	295.1	295a	11.5b	2.1b	83b
A78-123018		296	10.4	2.1	82
$LSD_{0.05}$[d]		6	0.6	0.1	2

[a]Expected yield based on the assumption of additive genetic control.

[b]Data from only two environments.

[c]Means followed by the same letter are not significantly (P>0.05) different, based on the Duncan's New Multiple Range Test.

[d]$LSD_{0.05}$ used to compare any backcross generation with the recurrent parent.

lines were significantly taller than the recurrent parent. The other backcross generations did not differ from the recurrent parent in plant height.

Combined analyses of variance for the Cumberland population indicated significant differences among lines within sets for all traits (Table 10). The mean squares for the lines within sets were partitioned into backcross generations within sets and lines within backcross generations within sets. Significant differences among backcross generations within sets and among lines within backcross generations within sets were found for all traits. The mean squares for lines within backcross generations within sets were further subdivided into mean squares for lines within each backcross generation. There was no significant difference for yield among lines within any backcross generation, except within the BC_1 generation. Significant differences for lodging and plant height were found in all backcross generations, except for plant height in the BC_2 and BC_3 generations. There was no significant difference among lines of any backcross generation for maturity, except in the BC_1 generation.

There was no significant difference among sets in the Cumberland population for any trait. Significant sets x environments interactions were detected for all traits. Significant differences among environments were found for all traits. Significant environments x lines within sets interactions were obtained for all traits. The mean squares for environments

Table 10. Analysis of variance for four traits of lines from the Cumberland population combined across three environments

Sources of Variation	df	Mean Squares			df[a]	Mean Squares
		Yield	Lodging	Height		Maturity
Environments (E)	2	1454297**	5525.50**	3380**	1	17546.78**
Sets (S)	3	486	27.63	143	3	28.92
Replications/S/E	12	4173**	173.72**	406**	8	82.35**
Lines/S	184	1071**	24.73**	73**	184	5.14**
Generations (G)/S	24	2013*	33.42**	243**	24	11.28**
L/G/S	160	930**	23.42**	47**	160	4.22**
$L/BC_0/S$	32	918	21.86**	72**	32	5.88
$L/BC_1/S$	32	1200**	27.72**	64**	32	5.23**
$L/BC_2/S$	32	696	26.56**	23	32	2.57
$L/BC_3/S$	32	874	16.58**	36	32	2.85
$L/BC_4/S$	32	961	24.40**	40**	32	4.57

E x S	6	6185**	76.07**	125**	3	29.13**
E x L/S	368	749**	7.98**	22**	184	2.55**
E x G/S	48	1088**	13.11**	37**	24	2.88**
E x L/G/S	320	698**	7.21*	19*	160	2.50**
E x L/BC_0/S	64	975**	6.23	19	32	3.54**
E x L/BC_1/S	64	528	10.52**	19	32	1.92
E x L/BC_2/S	64	686**	7.24	16	32	2.06*
E x L/BC_3/S	64	675**	7.19	24**	32	2.11*
E x L/BC_4/S	64	625*	4.88	18	32	2.89**
Error	600	438	5.61	16	400	1.37
CV (%)		6.0	11.7	4.1		3.6

[a]Data from only two environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

x lines within sets were partitioned into environments x backcross generations within sets and environments x lines within backcross generations within sets. Significant environments x backcross generations within sets and environments x lines within backcross generations within sets interactions were detected for all traits. The mean squares of the environments x lines within backcross generations within sets were further subdivided into environments x lines within each backcross generation. Significant interactions with environments were found for yield and maturity in all backcross generations, except in the BC_1 generation. There was no significant interaction with environments for lodging and plant height in any backcross generation, except in the BC_1 generation for lodging and in the BC_3 generation for plant height. All backcross generations interacted significantly with the environment in maturity, except the BC_1 generation.

Means combined over environments for the Cumberland population indicated no significant difference among backcross generations and the recurrent parent for yield (Table 11). The yield of the donor parent was significantly higher than that of the recurrent parent. The donor parent also had significantly later maturity and significantly taller plant height than the recurrent parent. All backcross generations had significantly earlier maturity than the recurrent parent, except the BC_0F_4- and the BC_2F_2-derived lines. Lodging score of all backcross generations was the same as that of the recurrent parent, except

Table 11. Means of the population, the donor parent, five backcross generations, and the recurrent parent for four traits of lines from the Cumberland population combined across three environments

Backcross Generation	Expected[a] Yield	Traits			
		Yield	Maturity[b]	Lodging	Height
	g m^{-2}	g m^{-2}	days	score	cm
Population mean		348	31.8	2.0	97
Williams 82		361	34.1	1.9	105
BC_0	306.5	349a[c]	32.2a	1.9c	100a
BC_1	325.2	347a	31.8b	2.0b	96c
BC_2	334.6	347a	31.9ab	2.0b	95c
BC_3	339.3	347a	31.7b	2.1a	98b
BC_4	341.6	351a	31.0c	2.0b	98b
Cumberland		344	32.4	2.0	98
$LSD_{0.05}$[d]		9	0.6	0.1	2
$LSD_{0.05}$[e]		16	1.0	0.2	3

[a]Expected yield based on the assumption of additive genetic control.

[b]Data from only two environments.

[c]Means followed by the same letter are not significantly P(>0.05) different, based on the Duncan's New Multiple Range Test.

[d]$LSD_{0.05}$ used only to compare any backcross generation with the recurrent parent.

[e]$LSD_{0.05}$ used to compare the recurrent parent with the donor parent.

for the BC_0F_4- and the BC_3F_2-derived lines. BC_0F_4-derived lines were significantly taller while BC_1F_3- and BC_2F_2-derived lines were significantly shorter than the recurrent parent. Plant height of the other backcross generations did not differ from that of the recurrent parent.

The coefficients of variation (CV), based on data combined across environments, were similar in both populations for all traits, except maturity (Tables 8 and 10). The highest CV, 13.3%, was for maturity in the A78-123018 population, and the lowest CV, 3.6%, for maturity in the Cumberland population. This difference can be accounted for by a higher error mean squares and a lower mean maturity in the A78-123018 population than in the Cumberland population.

In the A78-123028 population, 58% of the lines of the BC_0 generation were not significantly lower yielding than the recurrent parent (Table 12). At least 85% of the lines were not lower yielding than the recurrent parent in the subsequent generations. In the Cumberland population, over 90% of the lines of all backcross generations were not significantly lower yielding than the recurrent parent.

The highest yielding line of the BC_1, BC_2, and BC_4 generations was significantly higher yielding than the recurrent parent in the A78-123018 population (Table 13). The highest yielding line of each backcross generation of the Cumberland population was significantly higher than the recurrent parent (Table 14). The highest yielding line of the BC_4 generation was

Table 12. Range, frequency distribution for yield of lines better, equal, or worse than the recurrent parent, and the mean of the recurrent parent of the A78-123018 and Cumberland populations combined across three environments

Backcross Generation	Range or Mean	Frequency Distribution[a]		
		Worse	Equal	Better
	$g\ m^{-2}$	----- No. of lines- -----		
A78-123018 population:				
BC_0	253 - 306	15	21	0
BC_1	269 - 317	5	28	3
BC_2	267 - 323	2	33	1
BC_3	280 - 311	0	36	0
BC_4	276 - 327	3	32	1
A78-123018	296			
Cumberland population:				
BC_0	321 - 383	0	33	3
BC_1	310 - 372	2	31	3
BC_2	325 - 384	0	35	1
BC_3	317 - 373	2	32	2
BC_4	319 - 377	1	31	4
Cumberland	344			

[a]Based on LSD at the 0.05 probability level. For the A78-123018 population $LSD_{0.05}$ = 18, and for the Cumberland population $LSD_{0.05}$ = 22.

Table 13. Means for four traits of the highest yielding line of each backcross generation and the recurrent parent of the A78-123018 population combined across three environments

Entry Designation	Backcross Generation	Trait			
		Yield	Maturity	Lodging	Height
		g m^{-2}	days	score	cm
A86-404002	BC_0	306b[a]	11.2b	2.0b	81b
A86-403016	BC_1	317ab	12.7a	2.0b	91a
A86-403023	BC_2	323ab	10.2b	2.1ab	77b
A86-403033	BC_3	311ab	13.0a	2.2a	82b
A86-404037	BC_4	327a	13.5a	2.2a	83b
A78-123018		296	10.4	2.1	82
$LSD_{0.05}$[b]		18	1.4	0.2	5

[a]Means followed by the same letter are not significantly ($P>0.05$) different.

[b]$LSD_{0.05}$ used to compare the recurrent parent with any line.

Table 14. Means for four traits of the donor parent, the highest yielding line of each backcross generation, and the recurrent parent of the Cumberland population combined across three environments

Entry Designation	Backcross Generation	Trait			
		Yield	Maturity	Lodging	Height
		g m^{-2}	days	score	cm
Williams 82		361	34.1	1.9	105
A86-409006	BC_0	383a[a]	32.7a	1.9a	102a
A86-410018	BC_1	372a	33.5a	1.6b	94b
A86-410025	BC_2	384a	32.7a	2.0a	95b
A86-407033	BC_3	373a	32.0a	1.9a	96b
A86-408041	BC_4	377a	32.2a	2.0a	96b
Cumberland		344	32.4	2.0	98ab
$LSD_{0.05}$[b]		23	1.3	0.2	4
$LSD_{0.05}$[c]		16	1.0	0.2	3

[a]Means followed by the same letter are not significantly ($P>0.05$) different.

[b]$LSD_{0.05}$ used to compare the recurrent parent with any line.

[c]$LSD_{0.05}$ used to compare the recurrent parent with the donor parent.

significantly higher in yield than the highest yielding line in the BC_0 generation of the A78-123018 population, but no such difference was found when comparing any other backcross generations. There was also no significant difference in yield among the highest yielding lines of the different backcross generations of the Cumberland population.

The range in yield of each backcross generation did not show a consistent change across backcross generations in either the A78-123018 or the Cumberland population (Table 12). The Cumberland population had a higher average yield level, but the yield ranges of each backcross generation were generally similar in both populations.

The range between the latest and the earliest maturing line of each backcross generation decreased from 11 days in the BC_0 generation to 6.5 days in the BC_4 generation of the A78-123018 population (Table 15). The range was only 6.5 days in the BC_0 generation of the Cumberland population and showed no consistent decrease in further backcross generations. The percentage of lines not significantly different from the maturity of the recurrent parent was lower in the A78-123018 population than in the Cumberland population. Lines in the A78-123018 population tended to be slightly later maturing than the recurrent parent whereas lines in the Cumberland population tended to be slightly earlier than the recurrent parent.

At least 60% of the lines of both populations did not differ from the recurrent parent in lodging (Table 16). The average

Table 15. Range, frequency distribution for maturity of lines earlier, equal, and later than the recurrent, and the mean of the recurrent parent of the A78-123018 and Cumberland populations combined across three environments

Backcross Generation	Range or Mean	Frequency Distribution[a]		
		Earlier	Equal	Later
	days	- - - - - No. of lines - - - -		
A78-123018 population:				
BC_0	7.0 - 18.0	4	21	11
BC_1	7.5 - 16.2	4	26	6
BC_2	7.0 - 16.5	1	22	13
BC_3	9.5 - 16.2	0	21	15
BC_4	7.7 - 14.2	1	21	14
A78-123018	10.4			
Cumberland population:				
BC_0	27.7 - 34.2	4	29	3
BC_1	29.5 - 34.0	10	25	1
BC_2	30.2 - 33.2	4	32	0
BC_3	29.7 - 33.5	7	29	0
BC_4	28.2 - 33.5	15	21	0
Cumberland	32.4			

[a]Based on LSD at the 0.05 probability level. For the A78-123018 population $LSD_{0.05}$ = 1.4, and for the Cumberland population $LSD_{0.05}$ = 1.3.

Table 16. Range, frequency distribution for lodging of lines better, equal, and worse than the recurrent parent, and the mean of the recurrent parent of the A78-123018 and Cumberland populations combined across three environments

Backcross Generation	Range or Mean	Frequency Distribution[a]		
		Worse	Equal	Better
	score	----- No. of lines-	----	
A78-123018 population:				
BC_0	1.5 - 2.7	25	11	0
BC_1	1.7 - 2.3	15	20	1
BC_2	1.8 - 2.6	2	30	4
BC_3	1.9 - 2.6	3	23	10
BC_4	1.9 - 2.4	1	27	8
A78-123018	2.1			
Cumberland population:				
BC_0	1.6 - 2.4	12	20	4
BC_1	1.6 - 2.4	12	17	7
BC_2	1.7 - 2.6	9	18	9
BC_3	1.8 - 2.4	4	22	10
BC_4	1.7 - 2.6	7	20	9
Cumberland	2.0			

[a]Based on LSD at the 0.05 probability level. For the A78-123018 and Cumberland populations $LSD_{0.05} = 0.2$.

lodging of each backcross generation would not preclude the release of any backcross generation to replace the recurrent parent in both populations. At least half of the lines of each backcross generation did not differ from the recurrent parent in height in both populations (Table 17). Lines of both populations tended to become more uniform in height in later backcross generations.

Estimates of phenotypic correlations for all traits of each backcross generation were computed based on entry means across environments (Tables 18 and 19). Estimates of genotypic correlations were computed for those traits that had significant variability among lines (Tables 20 and 21). There was considerable variation in the magnitude of the correlation estimates among backcross generations. Phenotypic correlations between yield and maturity were generally positive and varied from 0.06 to 0.65 in the A78-123018 population and from -0.15 to 0.33 in the Cumberland population. Genotypic correlation between yield and maturity was 0.76 in the A78-123018 population and 0.49 in the Cumberland population.

Yield and lodging were positively correlated in the A78-123018 population and negatively correlated in the Cumberland population. Phenotypic correlations between yield and height ranged from -0.18 to 0.44 in the A78-123018 population and from -0.22 to 0.26 in the Cumberland population. Genotypic correlation between yield and height was 0.50 in the A78-123018 population and -0.03 in the Cumberland population. Phenotypic

Table 17. Range, frequency distribution for height of lines taller, equal, and shorter than the recurrent parent, and the mean of the recurrent parent of the A78-123018 and Cumberland populations combined across three environments

Backcross Generation	Range or Mean	Frequency Distribution[a]		
		Shorter	Equal	Taller
	cm	----No. of lines----		
A78-123018 population:				
BC_0	69 - 106	9	17	10
BC_1	72 - 94	7	21	8
BC_2	77 - 95	1	19	16
BC_3	78 - 95	0	26	10
BC_4	79 - 89	0	33	3
A78-123018	82			
Cumberland population:				
BC_0	94 - 108	3	21	12
BC_1	90 - 103	16	17	3
BC_2	90 - 100	17	19	0
BC_3	94 - 102	4	29	3
BC_4	92 - 102	4	30	2
Cumberland	98			

[a]Based on LSD at the 0.05 level of probability. For the A78-123018 population $LSD_{0.05} = 4$, and for the Cumberland population $LSD_{0.05} = 3$.

Table 18. Phenotypic correlations among four traits of lines from each backcross generation of the A78-123018 population combined across three environments

Backcross Generation	Traits Correlated					
	Yield x[a] Maturity	Yield x Lodging	Yield x Height	Maturity x[a] Lodging	Maturity x[a] Height	Lodging x Height
BC_0	0.06	0.19	-0.03	0.41*	0.66**	0.69**
BC_1	0.45**	0.39*	0.44**	0.39*	0.51**	0.69**
BC_2	0.38*	0.04	0.02	0.30	0.37*	0.67**
BC_3	0.65**	0.05	-0.18	0.34*	0.09	0.37*
BC_4	0.45**	0.14	0.18	0.15	0.58**	0.32

[a]Data from only two environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 19. Phenotypic correlations among four traits of lines from each backcross generation of the Cumberland population combined across three environments

Backcross Generation	Traits Correlated					
	Yield x[a] Maturity	Yield x Lodging	Yield x Height	Maturity x[a] Lodging	Maturity x[a] Height	Lodging x Height
BC_0	0.09	-0.05	0.12	0.35*	0.10	0.45**
BC_1	0.30	-0.43**	0.07	-0.06	-0.18	0.24
BC_2	0.33*	-0.32	-0.22	0.12	0.04	0.36*
BC_3	-0.15	-0.14	0.26	0.07	-0.07	-0.08
BC_4	0.16	-0.32	-0.14	0.25	0.22	0.33*

[a]Data from only two environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 20. Genotypic correlations among four traits of lines from each backcross generation of the A78-123018 population combined across three environments

Backcross Generation	Traits correlated[a]					
	Yield x[b] Maturity	Yield x Lodging	Yield x Height	Maturity x[b] Lodging	Maturity x[b] Height	Lodging x Height
BC_0	-	-	-	0.52	0.85	0.79
BC_1	0.76	0.67	0.50	0.50	0.65	0.85
BC_2	-	-	-	0.45	0.52	0.93
BC_3	-	-	-	-	0.03	0.60
BC_4	-	-	-	-	-	-

[a]Genotypic correlations were computed for traits with significant ($P>0.05$) genetic variances.

[b]Data from only two environments.

Table 21. Genotypic correlations among four traits of lines from each backcross generation of the Cumberland population combined across three environments

Backcross Generation	Traits Correlated[a]					
	Yield x[b] Maturity	Yield x Lodging	Yield x Height	Maturity x[b] Lodging	Maturity x[b] Height	Lodging x Height
BC_0	-	-	-	-	-	0.46
BC_1	0.49	-0.76	-0.03	-0.35	-0.61	0.15
BC_2	-	-	-	-	-	-
BC_3	-	-	-	-	-	-
BC_4	-	-	-	-	-	0.40

[a]Genotypic correlations were computed for traits with significant ($P>0.05$) genetic variances.

[b]Data from only two environments.

correlations between maturity and lodging were generaly positive. Genotypic correlations between maturity and lodging were positive in the A78-123018 population and negative in the Cumberland population. Phenotypic correlations between maturity and height were generally of higher magnitude in the A78-123018 population than in the Cumberland population. Genotypic correlations between maturity and height were positive in the A78-123018 population and negative in the Cumberland population. Phenotypic correlations between lodging and height ranged from 0.32 to 0.69 in the A78-123018 population and from -0.08 to 0.45 in the Cumberland population, while genotypic correlations ranged from 0.60 to 0.93 in the A78-123018 population and from 0.15 to 0.46 in the Cumberland population.

Estimates of genetic variance for all traits of each backcross generation were computed based on entry means across environments (Tables 22 and 23). Genotypic variances for yield were generaly higher in the Cumberland than in the A78-123018 population. The highest genetic variance for yield was detected in the BC_1 generation of both populations. Negative genetic variance estimates for yield were observed in the BC_2 and BC_3 generations of the A78-123018 populations and in the BC_0 generation of the Cumberland population. The negative estimate of genetic variance in the Cumberland population is mainly due to a large genotype x environment interaction. There was no consistent change in the magnitude of genetic variance for yield across backcross generations in either of the two

Table 22. Estimates of genetic variances for four traits of each backcross generation of the A78-123018 population with two replications at three environments

Backcross Generation	Expected % Germplasm of Recur. Parent	Trait			
		Yield	Maturity[a]	Lodging	Height
BC_0	50.0	56.0± 30.4	3.76± 1.06	4.15± 1.18	57.6±15.6
BC_1	75.0	66.1± 37.6	3.55± 1.04	1.25± 0.51	29.1± 8.6
BC_2	87.5	-7.6± 20.4	2.75± 0.79	1.19± 0.62	10.5± 3.8
BC_3	93.7	-14.8± 18.7	0.96± 0.56	0.65± 0.49	8.1± 2.9
BC_4	96.9	22.0± 36.0	1.29± 0.34	0.57± 0.41	1.3± 1.6

[a]Data from only two environments.

Table 23. Estimates of genetic variances for four traits of each backcross generation of the Cumberland population with two replications at three environments

Backcross Generation	Expected % Germplasm of Recur. Parent	Trait			
		Yield	Maturity[a]	Lodging	Height
BC_0	50.0	-9.5± 46.6	0.58± 0.41	2.60± 0.20	8.8± 2.9
BC_1	75.0	112.0± 50.8	0.83± 0.34	2.86± 1.16	7.5± 2.6
BC_2	87.5	1.6± 34.4	0.13± 0.20	3.22± 1.09	1.1± 1.0
BC_3	93.7	33.1± 40.0	0.18± 0.21	1.56± 0.70	2.0± 1.6
BC_4	96.9	56.0± 42.8	0.42± 0.33	3.25± 1.00	3.6± 1.7

[a]Data from only two environments.

populations. There was no estimate of negative genetic variance for maturity, lodging and height. The initial backcross generations of the A78-123018 population showed higher estimates of genetic variance for maturity, lodging and height than those of the Cumberland population. There was a consistent decrease in the amount of genetic variance from the BC_0 to the BC_4 generation for maturity, lodging and height in the A78-123018 population, but there was no change in the amount of genetic variance in the Cumberland population.

Broad-sense heritability estimates were computed on an entry-mean and on a plot-mean basis for each backcross generation of both populations (Tables 24 and 25). Heritability for yield was highest in the BC_1 generation of both populations. There was no consistent change across backcross generations in the magnitude of heritability for yield in either of the two populations. The A78-123018 population showed a decrease in the magnitude of heritability from the BC_0 to the BC_4 generation for maturity, lodging and height, but there was no change in the Cumberland population.

Combined analyses of variance for the bulks of lines from each backcross generation indicated significant differences among bulks for lodging and maturity, but not for yield or height, in the A78-123018 population (Table 26). There were significant differences among bulks for all traits, except lodging, in the Cumberland population (Table 27). Significant differences among environments were detected for all traits in both populations.

Table 24. Heritability estimates of four traits of the lines from each backcross generation of the A78-123018 population calculated on an entry-mean and a plot-mean basis with two replications at three environments

Backcross Generation	Trait			
	Yield	Maturity[a]	Lodging	Height
	- - - - - - - - - - - - - % - - - - - - - - - - - - -			
Entry-mean:				
BC_0	31.9	86.5	84.9	89.6
BC_1	45.8	83.6	61.0	82.9
BC_2	0.0	82.4	49.7	68.5
BC_3	0.0	47.4	35.1	67.1
BC_4	17.2	64.7	37.0	22.2
Plot-mean:				
BC_0	8.1	61.5	48.5	64.3
BC_1	13.9	58.0	21.3	49.3
BC_2	0.0	53.9	17.0	28.4
BC_3	0.0	22.5	10.0	25.3
BC_4	4.3	33.3	10.0	4.8

[a]Data from only two environments.

Table 25. Heritability estimates of four traits of the lines from each backcross generation of the Cumberland population calculated on an entry-mean and a plot-mean basis with two replications at three environments

Backcross Generation	Trait			
	Yield	Maturity[a]	Lodging	Height
	- - - - - - - - - - - % - - - - - - - - - - -			
Entry-mean:				
BC_0	0.0	39.6	71.4	73.6
BC_1	56.0	63.3	62.0	70.3
BC_2	1.4	19.8	72.7	30.3
BC_3	22.7	25.4	56.5	33.3
BC_4	34.9	36.7	77.6	55.0
Plot-mean:				
BC_0	0.0	19.1	30.5	33.5
BC_1	18.8	33.4	26.2	30.0
BC_2	0.3	6.9	33.4	6.7
BC_3	5.6	9.4	19.6	9.1
BC_4	9.5	16.4	36.7	17.7

[a]Data from only two environments.

Table 26. Analysis of variance for four traits of bulks of the lines from each backcross generation of the A78-123018 population combined across six environments

Sources of Variation	df	Mean Squares			df[a]	Mean Squares
		Yield	Lodging	Height		Maturity
Environments (L)	5	15047**	99.80**	832**	3	263.46**
Replications/L	6	129	7.08	32	4	5.00*
Entries (E)	4	517	10.10**	37	4	4.10*
E x L	20	291	2.11	38	12	1.11
Error	24	201	4.54	21	16	1.16
CV (%)		5.0	11.0	5.5		7.1

[a]Data from only four environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 27. Analysis of variance for four traits of bulks of the lines from each backcross generation of the Cumberland population combined across six environments

Sources of Variation	df	Mean Squares			df[a]	Mean Squares
		Yield	Lodging	Height		Maturity
Environments (L)	5	11122**	355.60**	995**	3	229.00**
Replications/L	6	1083**	8.76	15	4	1.62
Entries (E)[b]	5	853**	13.51	152**	5	25.80**
E x L	25	197	9.73**	21	15	4.95**
Error	30	153	3.76	15	20	1.17
CV (%)		4.3	9.7	3.7		3.7

[a]Data from only two environments.

[b]The donor parent was included in the analysis.

**Significant at the 0.01 probability level.

There were no significant bulks x environments interactions for any trait in the A78-123018 population. Bulks x environments interactions were significant for lodging and maturity in the Cumberland population.

The coefficients of variation (CV) were similar for all traits in both populations, except for maturity (Tables 26 and 27). The CV for maturity in the A78-123018 population was nearly twice as large as in the Cumberland population. This difference can be largely accounted for by the difference in the mean maturity between the two populations.

In order to include the recurrent parent in the analyses of variance, data were combined across locations in 1986 (Tables 28 and 29). These analyses showed no significant difference among entries for any trait of the A78-123018 population except for maturity. There was significant difference among entries for all traits of the Cumberland population, except for lodging. Significant differences among locations were detected for all traits in both populations, except for yield in the Cumberland population. There were no significant locations x entries interactions in these analyses.

The coefficients of variation (CV) for the data combined across locations in 1986 were similar between both populations for all traits, except yield (Tables 28 and 29). The CV for yield in the Cumberland population was less than the half of that of the A78-123018 population.

Means combined across locations in 1986 indicated that the

Table 28. Analysis of variance for four traits of bulks of the lines from each backcross generation and the recurrent parent of the A78-123018 population combined across three locations in 1986

Sources of Variation	df	Mean Squares			df[a]	Mean Squares
		Yield	Lodging	Height		Maturity
Locations (L)	2	39184**	15.90**	544**	1	91.12**
Replications/L	3	65	2.52	55	2	2.56*
Entries (E)	5	208	11.00	46	5	6.60**
L x E	10	107	3.25	34	5	0.24
Error	27	146	5.76	27	18	0.53
CV (%)		3.9	11.5	6.1		4.9

[a]Data from only two environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 29. Analysis of variance for four traits of bulks of the lines of each backcross generation, the recurrent parent, and the donor parent of the Cumberland population combined across three locations in 1986

Sources of Variation	df	Mean Squares			df[a]	Mean Squares
		Yield	Lodging	Height		Maturity
Locations (L)	2	2817	458.50**	272*	1	28.44**
Replications/L	3	2537**	5.51	33	2	0.94
Entries (E)	6	1339**	13.80	107*	6	7.78**
L x E	12	135	8.41	30	6	0.51
Error	30	267	6.06	19	20	0.79
CV (%)		1.7	10.5	4.0		3.2

[a]Data from only two environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

recurrent parent in the Cumberland population was significantly higher yielding than the donor parent and all bulk generations, except BC_3 (Table 30). There was no significant difference in yield among the bulks. However, the donor parent was significantly lower yielding than any bulk of this population.

There was no significant difference in maturity among bulks of either the A78-123018 or Cumberland population (Table 31). The recurrent parent in the A78-123018 population was significantly earlier in maturity than all bulks. Williams 82, in the Cumberland population, had significantly later maturity and taller plant height than all other entries, except for the height of the BC_3 generation.

Means combined over environments in both years indicated that Williams 82 was significantly lower yielding than all bulks of the Cumberland population (Table 32). There was no significant difference in yield among bulks of either of the two populations. The BC_0 bulk of the A78-123018 population was significantly later in maturity than the BC_1 and BC_3 bulks. There was no significant difference among bulks for maturity in the Cumberland population. However, Williams 82 was significantly later maturing than all bulks, except the BC_0.

There were significant differences among bulks of the A78-123018 population for lodging, however, the range among bulks was only 0.2 units (Table 32). There was no significant difference among bulks of the Cumberland population for lodging or among bulks of the A78-123018 population for height.

Table 30. Means for four traits of a bulk of the lines from each backcross generation, the donor parent, and the recurrent parent of the Cumberland population combined across three locations in 1986

Entry	Trait			
	Yield	Maturity[a]	Lodging	Height
	g m^{-2}	days	score	cm
Williams 82	279b[b]	31.0a	2.3[c]	118a
BC_0	309a	28.5b	2.1	108b
BC_1	314a	27.5b	2.3	107b
BC_2	314a	27.2b	2.2	109b
BC_3	315a	27.2b	2.5	112ab
BC_4	313a	27.2b	2.4	106b
Cumberland	330	27.6	2.3	107
$LSD_{0.05}$[d]	16	1.0	-	5

[a]Data from only two locations.

[b]Means followed by the same letter are not significantly ($P>0.05$) different, based on the Duncan's New Multiple Range Test.

[c]The mean squares for differences among entries were not significant at the 0.05 probability level, therefore, no Duncan's or LSD test were calculated.

[d]$LSD_{0.05}$ used to compare the recurrent parent with any other entry.

Table 31. Means for four traits of a bulk of the lines from each backcross generation, and the recurrent parent of the A78-123018 population combined across three locations in 1986

Entry	Trait			
	Yield	Maturity[a]	Lodging	Height
	g m^{-2}	days	score	cm
BC_0	297[b]	16.2a[c]	2.0[b]	87[b]
BC_1	308	15.2a	2.1	86
BC_2	314	15.2a	2.2	87
BC_3	303	15.5a	2.1	86
BC_4	313	15.2a	2.3	86
A78-123018	312	13.5	2.0	82
$LSD_{0.05}$[d]	-	0.7	-	-

[a]Data from only two locations.

[b]The mean squares for differences among entries were not significant at the 0.05 probability level, therefore, no Duncan's or LSD test were calculated.

[c]Means followed by the same letter are not significantly ($P>0.05$) different, based on the Duncan's New Multiple Range Test.

[d]$LSD_{0.05}$ used to compare the recurrent parent with any other entry.

Table 32. Means for four traits of a bulk of the lines from each backcross generation of the A78-123018 and Cumberland populations combined across six environments

Bulk	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A78-123018 population:				
BC_0	277[a]	16.2a[b]	1.8c	86[a]
BC_1	279	14.5bc	1.8c	83
BC_2	289	15.0ab	2.0a	86
BC_3	274	14.5bc	1.9b	83
BC_4	292	15.1ab	2.0a	83
Cumberland population:				
Williams 82	269b	32.1a	1.9[a]	110a
BC_0	289a	29.6ab	1.8	103bc
BC_1	294a	27.8b	1.9	100d
BC_2	297a	27.2b	2.0	102cd
BC_3	295a	27.8b	2.1	105b
BC_4	294a	28.2b	2.0	102cd

[a]The mean squares for differences among entries were not significant at the 0.05 probability level, therefore, no Duncan's test was calculated.

[b]Means followed by the same letter were not significantly ($P>0.05$) different, based on the Duncan's New Multiple Range Test.

Williams 82 was significantly taller than all bulks in the Cumberland population. There was also significant difference among bulks for height, however, the range was not larger than 5 cm.

Estimates of genetic effects among bulks were computed for all traits of both populations, based on entry means across environments (Table 33). There was very little genetic difference among bulks for maturity, lodging, and height, especially in the A78-123018 population. The Cumberland population presented higher estimates of genetic effects for maturity and height than the A78-123018 population. This can be partially attributed to the presence of the donor parent in that experiment.

Broad-sense repeatibility estimates were computed on an entry-mean and on a plot-mean basis for the bulks of both populations (Table 34). No estimate of repeatibility was computed for plant height in the A78-123018 population because the estimate of genetic effects for the trait was negative.

Table 33. Estimates of genetic effects of four traits from the bulks of lines of each backcross generation of the A78-123018 and Cumberland populations combined across six environments

Trait	Population	
	A78-123018	Cumberland
Yield	18.83 ± 25.92	54.66 ± 38.25
Maturity[a]	0.37 ± 0.20	2.60 ± 1.15
Lodging	0.66 ± 0.49	0.31 ± 0.64
Height	-0.08 ± 2.02	10.90 ± 6.78

[a]Data from only four environments.

Table 34. Repeatibility estimates of four traits of the bulks of lines from the A78-123018 and Cumberland populations computed on an entry-mean basis and a plot-mean basis with two replications at six environments

Type of Repeatibility	Trait			
	Yield	Maturity[a]	Lodging	Height
	- - - - - - - - - - % - - - - - - - - - -			
A78-123018 population:				
Entry-mean	43.7	71.8	63.5	-
Plot-mean	7.1	24.2	12.7	-
Cumberland population:				
Entry-mean	76.9	80.8	27.7	86.1
Plot-mean	23.8	45.9	4.4	37.7

[a]Data from only four environments.

DISCUSSION

Backcrossing major genes for resistance to Phytophthora into susceptible soybean cultivars has been a widely used approach for control of the pathogen. In the 1960s, the Rps_1 gene for resistance to Phytophthora was incorporated into several widely grown cultivars. In 1972, Phytophthora seemed to be under control (Schmitthenner, 1985). Since that time, new races of Phytophthora capable of infecting otherwise resistant cultivars have been continuously discovered. Likewise, new resistance genes have been identified. Under this scenario, the backcross method very likely will continue to be used in developing soybean cultivars with resistance to specific races of Phytophthora.

"A major difficulty in backcrossing is to know when to cease crossing and start bulking" (Knight, 1945). The goal of the present study was to determine the earliest generation in which the breeder can stop backcrossing when incorporating major genes for resistance to Phytophthora into susceptible soybean cultivars. The results indicate that extensive backcrossing is not necessary for developing Phytophthora resistant cultivars when an elite donor parent is used.

The unique aspect of this study was that it provided information to the plant breeder about the number of backcrosses required to recover the yield level of the recurrent parent when the donor parent is an acceptable cultivar. The results of the

present study demonstrate that a single cross is sufficient to obtain a satisfactory frequency of Phytophthora resistant lines that are potential substitutes for the recurrent parent. In the backcross study of Wilcox et al. (1971), none of the individual lines had the same yield level as the recurrent parent before the BC_2 generation. The disparity in results of the two studies is mainly due to the relative difference in yield between the donor and recurrent parents used. In the present study, the difference in yield between Cumberland and Williams 82 was less than 10%, while in the study of Wilcox et al. (1971) the difference was about 20%. The population size of each backcross generation was considerably larger in the present study than in the study of Wilcox et al. (1971). A better sampling of the variability within backcross generations may be another reason for obtaining individual lines with a yield comparable to that of the recurrent parent at earlier generations in the present study.

If the purpose of a backcross program is to find transgressive segregates for yield, one backcross may be useful in some populations. No backcross was necessary to obtain transgressive segregants in the Cumberland population while one backcross was needed in the A78-12ɔ018 population. Caution is required to interpret the frequency distribution of the Cumberland population because the yield of the recurrent parent was uncommonly low in the experiment with individual lines. Therefore, its relative position in the yield ranking may be

lower than its actual position, which leads to an overestimation of the number of lines significantly higher yielding than the recurrent parent. Compared with the number of lines with a yield equivalent to that of the recurrent parent, the frequency of apparent transgressive segregants is considerably low. More than one backcross did not result in a large increase in the frequency of transgressive segregants for yield. Furthermore, there was no advantage in making more than one backcross to increase the yield level of the transgressive segregants.

Wilcox et al. (1971) recommended seven backcrosses before releasing a Phytophthora-resistant cultivar by bulking phenotypically similar lines. Results of the present study indicate that this can be done at an earlier stage of the backcross program when an elite donor parent is used. In the A78-125018 population, individual lines with Phytophthora resistance had an average yield comparable to that of the recurrent parent after the first backcross (Table 9). In the experiment with individual lines of the Cumberland population, the BC_0 generation had an average yield comparable to that of the recurrent parent (Table 11). In the experiments with the bulks, no significant yield differences among backcross generations were observed in both populations (Table 32). However, the yield rankings generally suggested that the BC_0 generation was slightly lower in yield than the other generations or the recurrent parents. A t-test showed that, if the statistical probability level to assess differences among

backcross generations would be 0.3, instead of 0.05, the BC_0 generation would be significantly lower yielding than the BC_1 generation in the Cumberland population. Likewise, if the number of replications per environment would be six, instead of two, the BC_0 generation also would be significantly ($P>0.05$) lower yielding than the BC_1 generation.

In the experiment with individual lines, the recurrent parent of the Cumberland population yielded 5% less than the donor parent. Schmitthenner et al. (1970) reported a reduction of 8 to 16% in yield of cultivars susceptible to Phytophthora when grown in fields with a light infection of the pathogen. A light, undetectable presence of the disease may have been responsible for the low yield of the recurrent parent in the Cumberland population. However, in the same experiment, the backcross generations containing the gene for resistance to Phytophthora also yielded less than the donor parent. This suggests that genotype x environment interaction favored the yield of the donor parent. No such phenomenon was observed in the experiment with bulks. The donor parent yielded less than the recurrent parent in the experiment with bulks of the Cumberland population. Furthermore, the mean between the experiment with individual lines and the experiment with bulks showed that the recurrent parent was the highest yielding entry and that the yield decreased with the decrease in the proportion of germplasm of the recurrent parent among backcross generations (Table 35).

Table 35. Means for yield of each backcross generation, the donor and recurrent parents of the Cumberland population combined over the experiment with individual lines and the experiment with bulks in 1986

Entry	Yield
	$g\ m^{-2}$
Williams 82	320
BC0	329
BC1	330
BC2	330
BC3	331
BC4	332
Cumberland	337

The yield level of the recurrent parent was recovered at different rates in both populations. Recovery of the yield of the recurrent parent in the A78-123018 population was relatively close to the expected, assuming only additive genetic control for the character. Under this assumption, the BC_0 generation of the Cumberland population yielded more than expected, but the subsequent backcross generations yielded less. Yield did not increase after the first backcross in the Cumberland population.

Failure to recover the yield of the recurrent parent according to that expected with additive genetic control has been reported by Wilcox et al. (1971). They suggested several possible causes for the deviation from the additive model: an inadequate sample size, nonadditive genetic effects, or continued segregation of genes controlling yield. The population size used in the present study was large enough to obtain transgressive segregants for yield at the initial backcross generations, but it may not have been large enough to constitute a representative sample of each backcross generation. This possibility is worthy of consideration because some of the backcross generations had negative estimates of genetic variances without large estimates of genotype x environment interaction.

Genetic control of yield in soybean has been shown to be due primarily to additive and additive x additive effects, but significant dominance deviations also have been reported (Brim and Cockerham, 1961; Gates et al., 1960; Leffel and Weiss, 1958). However, attributing deviations from the additive model in

advanced backcross generations to nonadditive genetic effects is objectionable because the proportion of the genome in which nonadditive genetic effects can occur is reduced by one half with every generation of backcrossing. In the BC_4 generation, non-additive genetic effects can only occur in 6.25% of the genome.

Continued segregation for yield may have contributed to the deviations from the additive model found in the present study. Mahmud and Kramer (1951) estimated that the F_6 is the last generation in which soybean lines can be derived and still give significant differences in yield. Because the approach to homozygosity during backcrossing is at the same rate as with selfing (Briggs, 1935), the last backcross generation in which we may expect detectable segregation for yield is the BC_5, and the last generation evaluated in the present study was the BC_4, followed by one generation of selfing.

The effect of the gene for resistance to Phytophthora on other plant characteristics has been extensively investigated (Caviness and Walters, 1971; Walters and Caviness, 1968; Chou and Schmitthenner, 1974; Singh and Lambert, 1985). Incorporation of Phytophthora resistance in soybeans has been reported to increase plant height and lodging (Wilcox et al., 1971; Cooper and Waranyuwat, 1985). Cooper and Waranyuwat (1985) regarded the increased lodging as a cause for the reduction in yield. In the present study, differences between the recurrent parent and the backcross generations of the Cumberland population for lodging,

height, or maturity, do not seem to be sufficient causes for the yield differences observed between the recurrent parent and the advanced backcross generations of the Cumberland population. Likewise, individual high yielding segregants do not seem to have their agronomic traits affected by the $\underline{Rps}_k{}^1$ allele to such a degree as to preclude their use for replacing the recurrent parent. This is especially the case for lodging and height. In the A78-123018 population, some of the highest yielding lines are 2 to 3 days later in maturity than the recurrent parent. However, there would be no difficulty in finding Phytophthora-resistant lines in this population that are not later in maturity and not lower in yield than the recurrent parent.

Scientists have attributed the continuous appearance of new virulent races of Phytophthora to the selection pressure caused by extensively growing cultivars with a few race-specific resistance genes (Laviolette and Athow, 1981; Schmitthenner, 1985). Breeding for race-specific resistant cultivars may have been accompanied by a loss of genes conferring horizontal resistance. Vanderplank (1984) defined this as the Vertifolia effect. Buzzell and Anderson (1982) reported that selection for tolerance to Phytophthora, based on low plant loss, followed by backcrossing to include race-specific resistance, should avoid the Vertifolia effect and provide effective, long-term disease control. Walker and Schmitthenner (1984a) obtained some indication that genes conferring tolerance are linked to major-genes conferring resistance to Phytophthora. Therefore, if the

donor parent in a backcross program designed to transfer a gene for race-specific resistance to Phytophthora contains a larger number of genes conferring tolerance to other races than the recurrent parent, then a backcross-derived population, which is homozygous for resistance to certain a race, can be expected to have a higher level of tolerance to other races than the recurrent parent. Furthermore, if the linkage between tolerance and resistance genes is not large, a higher level of tolerance can be expected in a bulk of the BC_1 generation than in later backcross generations. Differences in tolerance to Phytophthora among backcross generations, where the parents differ markedly in tolerance, are worthy of investigation.

SUMMARY AND CONCLUSIONS

This study was designed to investigate the number of backcrosses required to obtain Phytophthora-resistant lines with the yield potential of the recurrent parent, and to determine in what backcross generation a bulk of phenotypically similar, Phytophthora-resistant lines will provide the same yield as that of the recurrent parent. The allele Rps_1^k, conferring resistance to specific races of Phytophthora megasperma Drechs. f. sp. glycinea Kuan and Erwin, was transferred from the cultivar Williams 82 to the cultivar Cumberland and the experimental line A78-123018. Four backcrosses were made to Cumberland and A78-123018. Thirty-six random resistant lines from each backcross generation were used in the experiments. Two experiments were carried out. One evaluated the individual lines for yield, maturity, height and lodging in three Iowa environments. The other experiment evaluated bulks of the lines from each backcross generation for the same traits in six Iowa environments.

On the average for the two populations, 75% of the lines of the BC_0 generation had a yield not significantly different from that of the recurrent parent. It was generally observed that the BC_1 generation had an average yield equivalent to that of the recurrent parent. Subsequent backcross generations were not higher yielding than the BC_1 generation. The highest yielding line of the BC_2, BC_3, or BC_4 generation was not higher yielding

than that of the BC_1 generation. Therefore, if the donor and recurrent parents differ in yield by 10% or less, a single cross is sufficient to develop a population from which a homozygous resistant line can be selected to replace the recurrent parent. Alternatively, the recurrent parent can be replaced by a bulk of homozygous resistant lines after one backcross, without the need of yield evaluation. If transgressive segregants for yield are desired, a single cross or one backcross seems advisable for developing a population. The results of this study do not encourage conducting more than one backcross to increase the frequency of transgressive segregants for yield, the yield level of the transgressive segregants, or the average yield of the backcross generation.

APPENDIX A: THEORY OF BACKCROSSING

The theoretical frequency of the genotype of the recurrent parent for a single locus in a backcross derived population is given by the formula $(2^n-1)/2^n$, where n is the number of backcross generations (Jennings, 1916). The frequency of the genotype of the nonrecurrent parent is 0 and that of the heterozygote is $1/2^n$. The percentage of genes of the recurrent parent increases with each backcross according to the formula $1-(1/2)^{n+1}$, where n is the number of backcross generations. According to this formula, the average increase in the number of genes of the recurrent parent in each backcross corresponds to the half of the number of genes of the nonrecurrent parent present in the previous generation. It is an "average" increase because within each backcross generation there is a range among plants for the number of genes from the recurrent parent that they carry. This variation among plants is dependent on the frequency of loci homozygous for alleles comming from the recurrent parent. The percentage of homozygosity in each backcross generation is the same as in selfing and can be described by the formula $[(2^m-1)/2^m]^n$, where m is either the number of generations of backcrossing or selfing, and n is the number of loci with contrasting alleles in the two parents. With backcrossing, the proportion of homozygous loci is the same as that of the recurrent parent (Briggs, 1935).

The above considerations assume that there is no selection

or linkage in the population. Selection of individuals that resemble the recurrent parent can increase the rate of recovery of its alleles (Briggs and Allard, 1953).

When a given gene is incorporated into the genome of the recurrent parent, the chromosomal segment being transferred may also contain other genes from the nonrecurrent parent. The length of the chromosomal segment linked to the gene being transferred will decrease with each backcross generation if crossing over occurs within it. Because the frequency of crossing over within a given chromosomal region is expected to decrease by decreasing its length, the rate of elimination of chromosomal material adjacent to the gene being transferred also can be expected to decrease with additional backcrosses. Bartlett and Haldane (1935) showed that the mean genetic length of a chromosome linked to each side of the gene being transferred, if the gene is not terminal, can be defined as $[(1-2^{-n})/n]$, where n is the number of backcross generations. Crow and Kimura (1970) showed that the length of the chromosome linked to the gene being transferred also depends on the breeding strategy used. A dominant gene can be transferred by successive crosses between the heterozygote and the recurrent parent. In this case, the mean length of the chromosome linked to the gene being transferred is approximately 100/t centimorgans on each side of the gene, or 200/t centimorgans altogether, where t is the number of backcrosses. If the gene being transferred is recessive and the backcrosses are alternated with selfings to identify the

plant carrying the desired gene, the mean length of the chromosome adjacent to this gene is approximately 200/t centimorgans on each side of the gene, or 400/t altogether. The proportion of the total genome that is still heterozygous can be estimated from the length of the chromosome attached to the gene under transfer and the total map length of the genome (Falconer, 1981).

The chromosome attached to the gene being transferred may include an undesirable gene. This undesirable gene can be eliminated from the genome if effective crossing over between it and the gene being transferred occurs. Harlan and Pope (1922) concluded that, if crossing over occurs in that region, it should be easier to obtain a desirable recombinant by backcrossing than from an extensive F_2 generation. Their reasoning can be illustrated by assuming that the allele A, to be transferred from the nonrecurrent parent, is linked to an undesirable allele b. Assume the genotype of those two loci to be aB. In each backcross generation, Ab gametes from the backcross progeny unite with the aB gametes from the recurrent parent to produce the genotype Ab/aB. If crossing over occurs between A and b, an AB gamete will be produced. On the other hand, if a selfing strategy is used, there will be an increase in the percentage of homozygous individuals in each generation. Crossing over between A and b in the homozygous genotype Ab/Ab or aB/aB will not result in the desired AB gamete.

The frequency of crossing over between the desired and the

undesired gene is related to the map distance between the genes. Bartlett and Haldane (1935) indicated that, after n generations of backcrossing, the probability of introducing an unlinked gene with the gene being transferred is given by 2^{1-n}. If the genes are linked, this probability becomes $(1-c)^{n-1}$, where c is the map distance between the genes, measured by the frequency of crossing over. The probability that the undesirable gene linked to the desired one will be eliminated during backcrossing was given by Allard (1960) as $1-(1-p)^{m+1}$, where p is the recombination fraction and m is the number of backcrosses. This formula assumes that no selection is practiced during backcrossing, except for the gene being transferred. Allard (1960) also uses this formula to illustrate the conclusion of Harlan and Pope (1922) that the probability of obtaining desirable recombination between the alleles of the locus being transferred and those of adjacent loci is higher with backcrossing than with selfing.

If a given A gene is to be transferred from an AA genotype into an aa background, there is a 50% chance that a given individual, after the initial cross, will carry the gene being transferred. In a backcross breeding program, the breeder wants to have a level of certainty, for example 95%, that the gene will be transferred from one generation to the next. The question, then, becomes: what is the number of plants necessary or how many BC_nF_1 seeds should be obtained to be 95% certain that the gene being transferred will be present in the next backcross generation. Sedcole (1977) presented a method of determining

the number of plants necessary to grow in such situations: $\Sigma^{n}_{i=r}\binom{n}{i}q^{i}(1-q)^{n-i}=p$, where n is the number of plants necessary; q is the probability of occurrence of the trait; and p is the probability of recovering r plants with the trait. An approximate estimate of n can be obtained by the formula $n=\{[2(r-0.5) + z^2(1-q)] + z[z^2(1-q)^2 + 4(1-q)(r-0.5)]^{1/2}\}/2q$, where n, r, and q are as given previously, and z is the normal deviate (Table A3 of Snedecor and Cochran, 1980). If only one plant with the desired trait is needed, the number of plants necessary is given by the formula $n=\log(1-p)/\log(1-q)$.

APPENDIX B: MEAN VALUES FOR FOUR TRAITS OF LINES FROM THE A78-123018 AND CUMBERLAND POPULATIONS AT INDIVIDUAL ENVIRONMENTS AND COMBINED ACROSS ENVIRONMENTS

Table B1. Means for four traits of lines from the A78-123018 and Cumberland populations at individual environments and combined across environments

Environment	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
A78-123018 population:				
Ames 1985	250	9.9	1.7	82
Ames 1986	343	13.0	2.1	86
Spencer 1986	279	-	2.4	83
Combined	291	11.4	2.1	84
$LSD_{0.05}$[a]	13	1.0	0.1	2
Cumberland population:				
Ames 1985	279	36.5	1.9	100
Stuart 1986	375	27.1	1.7	94
Ottumwa 1986	391	-	2.4	98
Combined	348	31.8	2.0	97
$LSD_{0.05}$[a]	12	1.4	0.2	3

[a] $LSD_{0.05}$ used to compare the mean of any environment with the combined mean.

APPENDIX C: SET MEANS FOR FOUR TRAITS OF LINES FROM THE A78-123018 AND CUMBERLAND POPULATIONS AT INDIVIDUAL ENVIRONMENTS AND COMBINED ACROSS ENVIRONMENTS

Table C1. Set means for four traits of lines from two populations combined across three environments

Set	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A78-123018 population:				
403	296	11.0	2.1	84
404	289	11.5	2.1	84
405	287	11.9	2.0	83
406	290	11.4	2.1	85
Cumberland population:				
407	347	31.7	2.0	96
408	348	32.1	2.0	98
409	348	32.1	2.0	97
410	349	31.3	2.0	98

[a]The mean squares for differences among sets were not significant at the 0.05 probability level for any trait in both populations, therefore, no Duncan's or LSD test were calculated.

Table C2. Set means for four traits of lines from the A78-123018 population at individual environments

Set	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
Ames 1985:				
403	263	9.9	1.8	83
404	247	9.7	1.7	82
405	246	10.5	1.6	81
406	246	9.5	1.7	84
Ames 1986:				
403	353	12.1	2.1	85
404	342	13.3	2.1	86
405	332	13.3	2.1	86
406	343	13.3	2.1	86
Spencer 1986:				
403	273	-	2.5	82
404	279	-	2.4	84
405	283	-	2.4	84
406	281	-	2.4	85

[a]The mean squares for differences among sets were not significant at the 0.05 probability level for any trait, therefore, no Duncan's or LSD test were calculated.

Table C3. Set means for four traits of lines from the Cumberland population at individual environments

Set	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Ames 1985:				
407	285a[a]	36.1[b]	1.8[b]	99[b]
408	283a	37.1	2.0	100
409	278ab	37.2	1.8	101
410	268b	35.7	1.8	99
Stuart 1986:[b]				
407	367	27.2	1.7	92
408	372	27.1	1.7	94
409	379	26.9	1.7	94
410	382	26.9	1.8	96
Ottumwa 1986:[b]				
407	389	-	2.5	98
408	389	-	2.4	98
409	388	-	2.4	97
410	399	-	2.5	99

[a]Means followed by the same letter are not significantly different at the 0.05 level of probabilty, based on the Duncan's New Multipla Range Test.

[b]The mean squares for differences among sets were not significant (P>0.05), therefore, no Duncan's test was calculated.

APPENDIX D: MEAN VALUES FOR FOUR TRAITS OF EACH BACKCROSS GENERATION FROM THE INDIVIDUAL LINES OF THE A78-123018 AND CUMBERLAND POPULATIONS AT INDIVIDUAL ENVIRONMENTS

Table D1. Means of five backcross generations and the recurrent parent for four traits of lines from the A78-123018 population at Ames in 1985

Backcross Generation	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
BC_0	235b	9.4c	1.5d	82a
BC_1	253a	9.8bc	1.6c	82a
BC_2	251a	10.4ab	1.7b	83a
BC_3	253a	10.5a	1.8a	83a
BC_4	258a	9.8bc	1.8a	82a
A78-123018	257	8.4	1.7	81
$LSD_{0.05}$[b]	10	0.8	0.1	2

[a]Means followed by the same letter are not significantly different at the 0.05 level of probability, based on the Duncan's New Multiple Range Test.

[b]$LSD_{0.05}$ used to compare any backcross generation with the recurrent parent.

Table D2. Means of five backcross generations and the recurrent parent for four traits of lines from the A78-123018 population at Ames in 1986

Backcross Generation	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
BC_0	328c	12.7b	2.0b	85b
BC_1	341b	12.3c	2.0b	84b
BC_2	345ab	13.4a	2.2a	88a
BC_3	350a	13.5a	2.2a	87a
BC_4	348a	13.2a	2.2a	85b
A78-123018	347ab	12.4	2.1	82
$LSD_{0.05}$[b]	9	0.5	0.1	2

[a]Means followed by the same letter are not significantly different at the 0.05 level of probability, based on the Duncan's New Multiple Range Test.

[b]$LSD_{0.05}$ used to compare any backcross generation with the recurrent parent.

Table D3. Means of five backcross generations and the recurrent parent for four traits of lines from the A78-123018 population at Spencer in 1986

Backcross Generations	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
BC0	277ab	-	2.2c	84a
BC1	281a	-	2.3b	82b
BC2	281a	-	2.5a	85a
BC3	274b	-	2.5a	85a
BC4	280a	-	2.5a	82b
A78-123018	284	-	2.4	81
$LSD_{0.05}$[b]	6		0.1	2

[a]Means followed by the same letter are not significantly different at the 0.05 level of probability.

[b]$LSD_{0.05}$ used to compare any backcross generation with the recurrent parent.

Table D4. Means of the donor parent, the five backcross generations, and the recurrent parent for four traits of lines from the Cumberland population at Ames in 1985

Backcross Generations	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Williams 82	290	36.7	1.7	103
BC_0	282a	36.6b	1.8c	101a
BC_1	281a	36.8b	1.9b	99b
BC_2	284a	36.6b	1.8c	97c
BC_3	274b	35.5c	2.0a	100ab
BC_4	274b	38.1a	1.9b	100ab
Cumberland	270	37.5	1.9	101
$LSD_{0.05}$[b]	9	0.7	0.1	2
$LSD_{0.05}$[c]	15	1.2	0.2	3

[a]Means followed by the same letter are not significantly different at the 0.05 level of probability, based on the Duncan's New Multiple Range Test.

[b]$LSD_{0.05}$ used to compare any backcross generation with the recurrent parent.

[c]$LSD_{0.05}$ used to compare the donor parent with the recurrent parent.

Table D5. Means of the donor parent, the five backcross generations, and the recurrent parent for four traits of lines from the Cumberland population at Stuart in 1986

Backcross Generation	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Williams 82	387	30.1	1.9	101
BC_0	371b	27.8a	1.7b	96a
BC_1	369b	27.1b	1.7b	92b
BC_2	374b	27.0b	1.7b	91b
BC_3	373b	26.8c	1.7b	95a
BC_4	384a	26.5d	1.8a	95a
Cumberland	383	27.3	1.6	95
$LSD_{0.05}$[b]	10	0.2	0.1	2
$LSD_{0.05}$[c]	17	0.4	0.2	3

[a]Means followed by the same letter are not significantly different at the 0.05 level of probability, based on the Duncan's New Multiple Range Test.

[b]$LSD_{0.05}$ used to compare any backcross generation with the recurrent parent.

[c]$LSD_{0.05}$ used to compare the donor parent with the recurrent parent.

Table D6. Means of the donor parent, the five backcross generations, and the recurrent parent for four traits of lines from the Cumberland population at Ottumwa in 1986

Backcross Generation	Trait[a]			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Williams 82	407	-	2.2	111
BC_0	394ab	-	2.2c	102a
BC_1	390bc	-	2.4b	97b
BC_2	385c	-	2.5a	95c
BC_3	393ab	-	2.5a	98b
BC_4	398a	-	2.5a	98b
Cumberland	381	-	2.4	97
$LSD_{0.05}$[b]	10		0.1	2
$LSD_{0.05}$[c]	18		0.2	3

[a]Means followed by the same letter are not significantly different at the 0.05 level of probability, based on the Duncan's New Multiple Range Test.

[b]$LSD_{0.05}$ used to compare any backcross generation with the recurrent parent.

[c]$LSD_{0.05}$ used to compare the donor parent with the recurrent parent.

APPENDIX E: ANALYSES OF VARIANCE FOR FOUR TRAITS OF INDIVIDUAL LINES OF THE A78-123018 AND CUMBERLAND POPULATIONS AT INDIVIDUAL ENVIRONMENTS

Table E1. Analysis of variance for four traits of lines from the A78-123018 population at Ames in 1985

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Sets (S)	3	6949	17.77	75.33	169
Replications/S	4	16094**	50.45**	75.00**	268**
Lines (L)/S	180	876**	8.63**	9.71**	68**
Generations (G)/S	20	1516**	8.88**	29.47**	57**
L/G/S	160	796**	8.58**	7.24**	68**
$L/BC_0/S$	32	753*	8.61**	7.61**	153**
$L/BC_1/S$	32	658	10.83**	7.26**	88**
$L/BC_2/S$	32	595	7.50**	6.80**	34
$L/BC_3/S$	32	736*	8.37**	6.47**	28
$L/BC_4/S$	32	1237**	7.62**	8.06**	37*
Error	196	504	3.49	3.74	24
CV (%)		8.9	18.8	11.4	5.9

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table E2. Analysis of variance for four traits of lines from the A78-123018 population at Ames 1986

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Sets (S)	3	6885	36.50	6.66	17
Replications/S	4	2751**	16.49**	36.07**	147**
Lines (L)/S	180	639**	7.07**	8.86**	93**
Generations (G)/S	20	1484**	7.43**	20.28**	145**
L/G/S	160	533**	7.01**	7.43**	86**
$L/BC_0/S$	32	590*	11.08**	10.81**	186**
$L/BC_1/S$	32	726**	9.37**	5.23	120**
$L/BC_2/S$	32	480	7.37**	6.90*	53**
$L/BC_3/S$	32	300	4.07**	8.56**	51**
$L/BC_4/S$	32	569*	3.20**	5.65	22
Error	196	383	1.21	4.20	27
CV (%)		5.7	8.4	9.6	6.1

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table E3. Analysis of variance for three traits of lines from the A78-123018 population at Spencer in 1986

Sources of Variation	df	Mean Squares		
		Yield	Lodging	Height
Sets (S)	3	1691	36.33	90
Replications/S	4	609**	39.14**	35
Lines (L)/S	180	290**	15.95**	69**
Generations (G)/S	20	550**	45.16**	79**
L/G/S	160	257**	12.29**	67**
$L/BC_0/S$	32	257*	19.22**	126**
$L/BC_1/S$	32	424**	9.34**	75**
$L/BC_2/S$	32	203	15.15**	62**
$L/BC_3/S$	32	171	10.52**	40**
$L/BC_4/S$	32	232	7.25	33*
Error	196	167	5.29	22
CV (%)		4.6	9.5	5.6

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table E4. Analysis of variance for four traits of lines from the Cumberland population at Ames in 1985

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Sets (S)	3	5808**	56.00	115.32	89
Replications/S	4	558	158.80**	267.13**	769**
Lines (L)/S	184	956**	5.96**	12.80**	28**
Generations (G)/S	24	1530**	7.67**	14.97**	53**
L/G/S	160	869**	5.69**	12.47**	24**
$L/BC_0/S$	32	1268**	7.78**	12.93**	30**
$L/BC_1/S$	32	678**	5.81**	17.21**	32**
$L/BC_2/S$	32	810**	3.93*	11.00**	19
$L/BC_3/S$	32	656**	4.10*	10.48**	22*
$L/BC_4/S$	32	934**	6.87**	10.74**	19
Error	200	362	2.42	5.63	13.9
CV (%)		6.8	4.2	12.6	3.7

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table E5. Analysis of variance for four traits of lines from the Cumberland population at Stuart in 1986

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Sets (S)	3	4320	2.13	37.80	268
Replications/S	4	9780**	5.90**	117.00**	228**
Lines (L)/S	184	714**	1.74**	11.75**	42**
Generations (G)/S	24	1151**	6.49**	8.04**	91**
L/G/S	160	648**	1.02**	11.75**	35**
$L/BC_0/S$	32	651	1.62**	11.01**	49**
$L/BC_1/S$	32	849**	1.34**	15.61**	42**
$L/BC_2/S$	32	509	0.70**	13.73**	25
$L/BC_3/S$	32	750*	0.86**	4.91	31*
$L/BC_4/S$	32	480	0.60**	13.50**	29*
Error	200	455	0.32	4.41	19
CV (%)		5.7	2.1	12.1	4.6

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table E6. Analysis of variance for four traits of lines from the Cumberland population at Ottumwa in 1986

Sources of Variation	df	Mean Squares		
		Yield	Lodging	Height
Sets (S)	3	2728	26.66	36
Replications/S	4	2181**	137.00**	220**
Lines (L)/S	184	899**	16.61**	45**
Generations (G)/S	24	1509**	36.63**	173**
L/G/S	160	808**	13.61**	26**
$L/BC_0/S$	32	948**	10.36*	31**
$L/BC_1/S$	32	728*	15.94**	28**
$L/BC_2/S$	32	748*	16.30**	10
$L/BC_3/S$	32	819*	15.50**	32**
$L/BC_4/S$	32	797*	9.94*	29**
Error	200	498	6.80	16
CV (%)		5.7	10.6	4.1

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

APPENDIX F: MEANS FOR FOUR TRAITS OF BULKS OF LINES FROM THE A78-123018 AND CUMBERLAND POPULATIONS AT INDIVIDUAL ENVIRONMENTS AND COMBINED ACROSS ENVIRONMENTS

Table F1. Means for four traits of bulks from the lines of the A78-123018 population at individual environments and combined across environments

Environment	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Ames 1985	244	8.6	1.6	83
Corwith 1985	273	20.7	2.1	94
Manson 1985	256	-	1.5	69
Ames 1986	376	13.0	2.0	92
Corwith 1986	289	16.4	2.0	82
Spencer 1986	262	-	2.2	81
Combined	283	15.1	1.9	84
$LSD_{0.05}$[a]	5	1.0	0.1	3

[a]$LSD_{0.05}$ used to compare any individual environment mean with the combined mean.

Table F2. Means for four traits of bulks from the lines of the Cumberland population at individual environments and combined across environments

Environment	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
Ames 1985	218	34.7	1.2	89
Stuart 1985	286	24.3	1.9	98
Ottumwa 1985	309	-	1.7	106
Ames 1986	313	28.8	2.6	113
Stuart 1986	301	27.0	1.7	105
Ottumwa 1986	331	-	2.5	109
Combined	290	28.8	2.0	104
$LSD_{0.05}$[a]	12	1.0	0.1	2

[a] $LSD_{0.05}$ used to compare any individual environment mean with the combined mean.

APPENDIX G: MEANS FOR FOUR TRAITS OF A BULK OF THE LINES FROM EACH BACKCROSS GENERATION OF THE A78-123018 AND CUMBERLAND POPULATIONS AT INDIVIDUAL ENVIRONMENTS

Table G1. Means for four traits of a bulk of the lines from each backcross generation of the A78-123018 population at individual environments

Bulk	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Ames 1985:				
BC_0	247ab[a]	10.5[b]	1.4[b]	90a[a]
BC_1	238bc	7.5	1.4	79b
BC_2	258a	9.5	1.7	89a
BC_3	228c	7.5	1.6	75b
BC_4	246ab	8.0	1.7	79b
Manson 1985:[b]				
BC_0	260	-	1.4	72
BC_1	240	-	1.3	67
BC_2	250	-	1.5	73
BC_3	227	-	1.6	64
BC_4	306	-	1.6	70

[a]Means followed by the same letter are not significantly different (P>0.05), based on the Duncan's New Multiple Range Test.

[b]The mean squares for differences among backcross generations were not significant at the 0.05 probability level, therefore, no Duncan's or LSD test were calculated.

Table G1. (continued)

Bulk	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Corwith 1985:[b]				
BC_0	266	22.0	1.9	92
BC_1	271	20.0	2.0	95
BC_2	285	20.0	2.1	94
BC_3	280	19.5	2.2	99
BC_4	262	22.0	2.1	89
Ames 1986:				
BC_0	358[b]	14.5a[a]	2.1[b]	88[b]
BC_1	374	13.5a	2.2	98
BC_2	376	13.5a	2.1	93
BC_3	366	14.0a	1.9	92
BC_4	397	14.0a	2.2	99
A78-123018	381	11.6	1.8	88
$LSD_{0.05}$[c]	-	1.7	-	-

[c] $LSD_{0.05}$ used to compare any generation mean with the recurrent parent.

Table G1. (continued)

Bulk	Trait			
	Yield	Maturity	Lodging	Height
	g m-2	days	score	cm
Spencer 1986:				
BC_0	255[b]	-	2.1bc[a]	85[b]
BC_1	267	-	2.0c	81
BC_2	264	-	2.2bc	83
BC_3	260	-	2.3ab	84
BC_4	266	-	2.5a	79
A78-123018	261	-	2.1	79
$LSD_{0.05}$[c]	-	-	0.2	-
Corwith 1986:				
BC_0	278[b]	18.0a[a]	2.0[b]	89[b]
BC_1	284	17.0b	2.1	79
BC_2	302	17.0b	2.2	86
BC_3	284	17.0b	2.0	83
BC_4	279	16.5b	2.1	81
A78-123018	295	15.3	2.0	80
$LSD_{0.05}$[c]	-	0.8	-	-

Table G2. Means for four traits of the bulks of lines from each backcross generation of the Cumberland population at individual environments

Bulk	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Ames 1985:				
Williams 82	202b[a]	37.0a[a]	1.3[b]	93[b]
BC_0	213b	36.5a	1.2	90
BC_1	235a	31.0b	1.2	87
BC_2	238a	32.0b	1.2	82
BC_3	204b	36.0a	1.2	91
BC_4	221ab	36.0a	1.2	90
Stuart 1985:				
Williams 82	266[b]	29.5a[a]	1.3[b]	103[b]
BC_0	280	25.0ab	1.9	98
BC_1	294	25.5ab	1.8	95
BC_2	301	22.5b	2.4	99
BC_3	296	21.0b	2.0	98
BC_4	282	22.5b	2.0	96

[a]Means followed by the same letter are not significantly different (P>0.05), based on the Duncan's New Multiple Range Test.

[b]Mean squares for differences among bulks were not significant (P>0.05), therefore, no Duncan's or LSD test were calculated.

Table G2. (continued)

Bulk	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Ottumwa 1985:[a]				
Williams 82	311ab	-	1.8b	113a
BC_0	309bc	-	1.6d	109ab
BC_1	295d	-	1.5e	99c
BC_2	298cd	-	1.8b	105bc
BC_3	322a	-	1.9a	108ab
BC_4	319ab	-	1.7c	105bc
Ames 1986:				
Williams 82	267[b]	31.5[b]	2.4[b]	126a[a]
BC_0	290	29.0	2.4	110b
BC_1	318	28.5	2.9	108b
BC_2	315	28.0	2.6	118ab
BC_3	319	28.0	3.0	118ab
BC4	315	28.0	2.6	105b
Cumberland	330	28.8	2.7	110
$LSD_{0.05}$[c]	-	-	-	10

[c] $LSD_{0.05}$ used to compare the recurrent parent with any entry.

Table G2. (continued)

Bulk	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Stuart 1986:				
Williams 82	277[b]	30.5a[a]	2.2a[a]	109[b]
BC_0	295	28.0b	1.4d	104
BC_1	305	26.5c	1.5cd	104
BC_2	296	26.5c	1.6bcd	103
BC_3	298	26.5c	2.0ab	104
BC_4	296	26.5c	1.9abc	106
Cumberland	314	26.3	1.6	105
$LSD_{0.05}$[c]	-	1.0	0.4	-
Ottumwa 1986:				
Williams 82	294	-	2.5	118a
BC_0	345	-	2.4	109bc
BC_1	320	-	2.5	108bc
BC_2	332	-	2.6	105c
BC_3	329	-	2.6	113ab
BC_4	326	-	2.8	108bc
Cumberland	345	-	2.5	107
$LSD_{0.05}$[c]	-	-	-	6

APPENDIX H: ANALYSES OF VARIANCE FOR FOUR TRAITS OF THE BULKS FROM LINES OF EACH BACKCROSS GENERATION OF THE A78-123018 AND CUMBERLAND POPULATIONS AT INDIVIDUAL ENVIRONMENTS

Table H1. Analysis of variance for four traits of bulks of the lines of each backcross generation of the A78-123018 population at individual environments

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Ames 1985:					
Replications	1	612**	10.00*	14.40	137**
Entries	4	178*	3.60	4.15	89**
Error	4	20	1.00	5.65	5
CV (%)		1.8	11.6	15.0	2.8
Corwith 1985:					
Replications	1	34	4.90	1.60	32
Entries	4	126	2.90	2.65	27
Error	4	161	3.40	0.85	25
CV (%)		4.6	8.9	4.4	5.4
Manson 1985:					
Replications	1	8	-	0.10	1
Entries	4	1221	-	2.60	29
Error	4	624	-	3.10	25
CV (%)		9.7	-	11.8	7.2

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table H1. (continued)

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Ames 1986:					
Replications	1	30	5.06*	5.06	138
Entries	5	245	4.02*	9.82	63
Error	9	208	0.86	10.31	55
CV (%)		3.8	7.1	16.0	8.1
Spencer 1986:					
Replications	1	34	-	0.25	25*
Entries	5	26	-	5.92*	17*
Error	9	87	-	1.12	5
CV (%)		3.5	-	4.8	2.7
Corwith 1986:					
Replications	1	130	0.06	2.25	4
Entries	5	151	2.82**	1.75	35
Error	9	145	0.19	5.86	21
CV (%)		4.1	2.7	11.7	5.5

Table H2. Analysis of variance for four traits of the bulks from lines of each backcross generation of the Cumberland population at individual environments

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Ames 1985:					
Replications	1	443*	2.08	0.33	4
Entries	5	315*	13.14**	0.33	27
Error	5	63	0.48	0.13	24
CV (%)		3.6	2.0	2.9	5.5
Stuart 1985:					
Replications	1	2	1.33	14.08*	30*
Entries	5	229	18.53*	23.28**	13
Error	5	63	2.93	2.08	3
CV (%)		2.8	7.0	7.5	1.7
Ottumwa 1985:					
Replications	1	49	-	0.33	14
Entries	5	162*	-	4.20*	42*
Error	5	23	-	0.73	8
CV (%)		1.5	-	4.9	2.7

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table H2. (continued)

Sources of Variation	df	Mean Squares			
		Yield	Maturity	Lodging	Height
Ames 1986:					
Replications	1	402	1.38	16.05	57
Entries	6	805	3.11	10.52	116*
Error	10	297	1.24	12.24	30
CV (%)		5.5	3.8	13.9	4.8
Stuart 1986:					
Replications	1	3516**	0.50	0.50	27
Entries	6	277	5.18**	17.16*	8
Error	10	277	0.33	4.50	17
CV (%)		5.5	2.1	12.1	4.0
Ottumwa 1986:					
Replications	1	3693**	-	0.00	18
Entries	6	527	-	2.94	42*
Error	10	227	-	1.43	11
CV (%)		4.5	-	4.6	3.0

APPENDIX I: MEAN VALUES FOR FOUR TRAITS OF EACH INDIVIDUAL LINE OF THE A78-123018 AND CUMBERLAND POPULATIONS COMBINED ACROSS ENVIRONMENTS

Table I1. Mean values for four traits of the recurrent parent, donor parent, and BC_0F_4-derived lines from the A78-123018 population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
A78-123018	296	10.4	2.1	82
Donor Parent				
Williams 82[a]	361	34.1	1.9	105
BC_0F_4-derived Lines				
A86-403001	290	10.7	1.9	92
A86-403002	289	10.7	2.1	81
A86-403003	275	11.2	2.0	87
A86-403004	287	8.0	1.7	73
A86-403005	277	7.5	1.6	69
A86-403006	278	12.5	2.2	96
A86-403007	286	12.2	2.1	94
A86-403008	294	9.2	1.8	76
A86-403009	277	11.5	2.0	91
A86-404001	281	12.0	2.0	79
A86-404002	305	11.2	2.0	81
A86-404003	275	9.5	1.6	73
A86-404004	294	11.2	1.8	73
A86-404005	275	11.5	1.7	95
A86-404006	274	9.2	1.8	77
A86-404007	281	11.2	2.0	83
A86-404008	256	11.2	1.9	85
A86-404009	270	13.5	1.8	83

[a]Data from the Cumberland population.

Table I1. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A86-405001	280	11.7	1.9	90
A86-405002	278	10.5	1.8	81
A86-405003	266	12.7	1.5	84
A86-405004	290	12.2	1.6	79
A86-405005	284	12.7	2.0	83
A86-405006	285	9.0	1.5	76
A86-405007	294	8.5	1.9	83
A86-405008	253	9.7	1.6	74
A86-405009	275	13.2	1.8	88
A86-406001	278	12.5	1.7	8
A86-406002	277	9.7	1.9	8
A86-406003	270	10.5	1.9	8
A86-406004	273	7.0	1.6	7
A86-406005	280	18.0	2.7	10
A86-406006	272	9.2	1.8	8
A86-406007	279	11.5	2.1	8
A86-406008	288	12.5	1.8	8
A86-406009	288	13.2	1.9	9
$LSD_{0.05}$ [b]	18	1.4	0.2	4

[b] $LSD_{0.05}$ used to compare any BC_0F_4-derived line with the recurrent parent.

Table I2. Mean values for four traits of the recurrent parent, donor parent, and BC_1F_3-derived lines from the A78-123018 population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
A78-123018	296	10.4	2.1	82
Donor Parent				
Williams 82[a]	361	34.1	1.9	105
BC_1F_3-derived Lines				
A86-403010	297	10.5	2.0	90
A86-403011	307	12.0	1.9	80
A86-403012	301	9.5	1.9	73
A86-403013	299	11.5	2.1	90
A86-403014	301	14.5	2.3	94
A86-403015	285	9.0	1.9	90
A86-403016	317	12.7	2.0	91
A86-403017	280	7.5	1.8	77
A86-403018	275	9.7	1.9	82
A86-404010	298	9.2	2.1	85
A86-404011	294	10.2	2.0	85
A86-404012	273	8.7	1.9	79
A86-404013	272	12.0	1.8	80
A86-404014	293	10.0	2.1	85
A86-404015	283	11.2	1.9	75
A86-404016	285	16.2	2.1	91
A86-404017	285	11.0	2.1	87
A86-404018	281	12.0	2.0	83

[a]Data from the Cumberland population.

Table I2. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A86-405010	278	8.5	1.9	72
A86-405011	302	14.0	2.0	84
A86-405012	269	10.7	2.0	80
A86-405013	270	8.5	2.0	82
A86-405014	293	11.0	1.8	78
A86-405015	294	11.7	1.8	80
A86-405016	288	15.5	2.2	88
A86-405017	277	11.5	1.7	7
A86-405018	291	11.5	1.9	8
A86-406010	279	9.2	1.9	7
A86-406011	315	14.5	2.2	8
A86-406012	282	11.5	1.8	8
A86-406013	293	8.7	1.7	7
A86-406014	309	11.5	2.0	8
A86-406015	314	11.0	2.0	8
A86-406016	309	10.5	2.0	9
A86-406017	294	11.0	1.7	8
A86-406018	301	9.7	1.8	7
$LSD_{0.05}$ [b]	18	1.4	0.2	4

[b] $LSD_{0.05}$ used to compare any BC_1F_3-derived line with the recurrent parent.

Table I3. Mean values for four traits of the recurrent parent, donor parent, and BC_2F_2-derived lines from the A78-123018 population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
A78-123018	296	10.4	2.1	82
Donor Parent				
Williams 82[a]	361	34.1	1.9	105
BC_2F_2-derived Lines				
A86-403019	308	11.5	2.1	84
A86-403020	296	7.0	1.9	78
A86-403021	296	10.0	2.3	87
A86-403022	305	11.2	2.2	81
A86-403023	323	10.2	2.1	77
A86-403024	306	11.7	2.2	88
A86-403025	303	10.2	2.1	78
A86-403026	308	12.0	2.6	82
A86-403027	304	11.0	2.1	81
A86-404019	294	12.5	2.0	82
A86-404020	292	10.0	2.2	83
A86-404021	286	12.0	2.1	83
A86-404022	291	12.5	2.0	83
A86-404023	291	11.7	2.0	85
A86-404024	298	10.7	2.0	82
A86-404025	287	11.7	2.0	82
A86-404026	301	14.2	2.0	84
A86-404027	306	15.7	2.5	95

[a]Data from the Cumberland population.

Table I3. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
A86-405019	282	15.7	2.1	8
A86-405020	277	9.7	1.7	8
A86-405021	284	12.2	2.1	8
A86-405022	267	12.7	2.1	8
A86-405023	273	10.7	2.1	8
A86-405024	277	16.5	2.0	8
A86-405025	292	15.0	2.1	9
A86-405026	302	11.5	2.1	8
A86-405027	284	13.0	2.0	8
A86-406019	283	11.5	2.0	8
A86-406020	290	12.7	2.1	9
A86-406021	299	15.0	2.0	8
A86-406022	278	10.5	2.4	9
A86-406023	281	11.5	2.2	9
A86-406024	292	10.7	2.0	8
A86-406025	288	12.2	1.9	84
A86-406026	281	10.2	2.1	92
A86-406027	294	10.2	1.9	81
$LSD_{0.05}$[b]	18	1.4	0.2	4

[b] $LSD_{0.05}$ used to compare any BC_2F_2-derived line with the recurrent parent.

Table I4. Mean values for four traits of the recurrent parent, donor parent, and BC_3F_2-derived lines from the A78-123018 population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
A78-123018	296	10.4	2.1	82
Donor Parent				
Williams 82[a]	361	34.1	1.9	105
BC_3F_2-derived Lines				
A86-403028	298	11.0	2.2	84
A86-403029	285	10.0	2.4	87
A86-403030	291	13.5	2.5	85
A86-403031	300	11.7	2.1	83
A86-403032	286	12.7	2.3	86
A86-403033	310	13.0	2.2	82
A86-403034	291	11.5	2.5	77
A86-403035	301	12.7	2.4	81
A86-403036	290	10.5	2.4	86
A86-404028	285	12.2	2.2	90
A86-404029	280	10.5	2.1	95
A86-404030	290	11.2	2.2	91
A86-404031	290	11.2	2.1	87
A86-404032	301	12.2	2.1	86
A86-404033	300	11.5	2.1	82
A86-404034	288	11.2	2.0	81
A86-404035	290	15.2	2.1	88
A86-404036	284	10.2	2.1	85

[a]Data from the Cumberland population.

Table I4. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A86-405028	286	11.7	2.1	8
A86-405029	303	12.7	2.1	8
A86-405030	285	10.7	1.9	8
A86-405031	286	12.0	2.1	8
A86-405032	298	12.0	2.0	8
A86-405033	301	14.2	2.2	9
A86-405034	290	12.7	2.2	8
A86-405035	284	12.7	2.0	8
A86-405036	290	11.5	2.0	8
A86-406028	288	9.5	2.2	88
A86-406029	292	11.0	2.2	90
A86-406030	283	11.2	1.9	83
A86-406031	309	13.5	2.2	83
A86-406032	296	12.2	2.6	85
A86-406033	285	12.0	1.9	80
A86-406034	293	12.7	2.1	85
A86-406035	291	11.7	1.9	82
A86-406036	292	16.2	2.3	85
$LSD_{0.05}$ [b]	18	1.4	0.2	4

[b] $LSD_{0.05}$ used to compare any BC_3F_2-derived line with the recurrent parent.

Table I5. Mean values for four traits of the recurrent parent, donor parent, and BC_4F_2-derived lines from the A78-123018 population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
A78-123018	296	10.4	2.1	82
Donor Parent				
Williams 82[a]	361	34.1	1.9	105
BC_4F_2-derived lines				
A86-403037	309	14.0	2.1	86
A86-403038	288	11.5	2.1	80
A86-403039	287	10.2	2.0	80
A86-403040	297	10.2	2.0	83
A86-403041	306	11.0	2.2	86
A86-403042	302	12.5	2.1	79
A86-403043	311	12.2	2.1	84
A86-403044	305	12.2	2.3	82
A86-403045	288	9.5	2.0	81
A86-404037	327	13.5	2.2	83
A86-404038	293	10.7	2.3	81
A86-404039	285	10.7	2.1	83
A86-404040	297	11.0	2.3	82
A86-404041	306	9.7	2.1	81
A86-404042	299	11.7	2.0	81
A86-404043	289	12.0	2.1	80
A86-404044	282	10.5	2.2	86
A86-404045	276	11.5	2.2	82

[a]Data from the Cumberland population.

Table I5. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A86-405037	291	12.7	1.9	8
A86-405038	290	13.2	2.0	8
A86-405039	300	11.7	1.9	8
A86-405040	286	11.0	2.1	8
A86-405041	310	12.0	2.3	8
A86-405042	298	9.7	2.1	8
A86-405043	276	12.2	2.0	8
A86-405044	313	14.2	2.2	8
A86-405045	290	11.7	2.0	8
A86-406037	276	12.7	2.4	87
A86-406038	293	10.0	2.0	81
A86-406039	286	12.2	2.3	89
A86-406040	303	12.2	2.3	83
A86-406041	285	7.7	2.1	80
A86-406042	294	10.0	2.2	81
A86-406043	288	11.2	2.0	85
A86-406044	297	12.2	2.0	82
A86-406045	292	13.5	1.9	83
$LSD_{0.05}$ [b]	18	1.4	0.2	4

[b] $LSD_{0.05}$ used to compare any BC_4F_2-derived line with the recurrent parent.

Table I6. Mean values for four traits of the recurrent parent, donor parent, and BC_0F_4-derived lines from the Cumberland population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
Recurrent Parent				
Cumberland	344	32.4	2.0	98
Donor Parent				
Williams 82	361	34.1	1.9	105
BC_0F_4-derived Lines				
A86-407001	332	31.7	1.6	95
A86-407002	339	31.5	1.7	95
A86-407003	351	32.7	1.7	102
A86-407004	347	32.7	2.0	98
A86-407005	357	32.7	2.0	100
A86-407006	346	29.5	1.6	101
A86-407007	372	34.2	1.8	104
A86-407008	359	32.7	1.8	104
A86-407009	344	33.0	1.7	95
A86-408001	351	32.0	2.0	101
A86-408002	347	33.0	2.0	108
A86-408003	321	31.7	2.1	102
A86-408004	341	32.2	2.1	103
A86-408005	348	32.7	1.6	94
A86-408006	324	32.0	1.8	100
A86-408007	335	34.0	1.9	102
A86-408008	349	33.0	1.7	101
A86-408009	355	33.7	2.3	99

Table I6. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A86-409001	359	30.7	1.7	94
A86-409002	328	34.0	1.9	98
A86-409003	359	33.5	2.4	105
A86-409004	355	31.7	1.9	94
A86-409005	348	33.2	2.0	104
A86-409006	383	32.7	1.8	102
A86-409007	346	32.0	1.8	100
A86-409008	374	33.2	1.8	98
A86-409009	363	32.7	1.6	97
A86-410001	338	32.2	1.9	99
A86-410002	351	27.7	1.9	101
A86-410003	356	32.5	2.0	95
A86-410004	348	31.2	1.8	101
A86-410005	334	32.7	2.3	101
A86-410006	343	31.7	1.7	95
A86-410007	342	31.7	2.0	101
A86-410008	358	30.0	1.8	98
A86-410009	354	32.2	1.9	97
$LSD_{0.05}$[a]	22	1.3	0.2	3
$LSD_{0.05}$[b]	16	1.0	0.2	3

[a] $LSD_{0.05}$ used to compare any BC_0F_4-derived line with the recurrent parent.

[b] $LSD_{0.05}$ used to compare the donor parent with the recurrent parent.

Table I7. Mean values for four traits of the recurrent parent, donor parent, and BC_1F_3-derived lines from the Cumberland population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
Cumberland	344	32.4	2.0	98
Donor Parent				
Williams 82	361	34.1	1.9	105
BC_1F_3-derived Lines				
A86-407010	342	32.0	2.0	94
A86-407011	364	33.7	1.8	94
A86-407012	357	29.5	1.6	92
A86-407013	360	32.7	1.9	96
A86-407014	368	33.0	1.7	94
A86-407015	310	30.7	2.1	92
A86-407016	350	32.0	1.8	96
A86-407017	317	30.2	2.3	92
A86-407018	346	32.5	2.2	98
A86-408010	348	31.5	1.8	99
A86-408011	354	32.0	1.9	98
A86-408012	329	32.7	2.3	97
A86-408013	348	31.5	1.9	97
A86-408014	362	33.0	2.1	97
A86-408015	347	31.2	1.8	94
A86-408016	337	31.2	2.0	98
A86-408017	348	32.2	1.8	90
A86-408018	351	33.2	2.1	96

Table I7. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
A86-409010	342	33.0	1.6	93
A86-409011	348	33.0	1.8	93
A86-409012	348	30.0	1.8	102
A86-409013	335	32.5	2.3	94
A86-409014	337	34.0	2.1	90
A86-409015	353	30.7	1.9	94
A86-409016	358	33.2	2.2	102
A86-409017	339	32.7	1.9	101
A86-409018	351	32.0	2.4	98
A86-410010	334	31.5	1.7	96
A86-410011	336	31.2	1.9	93
A86-410012	369	30.7	2.1	98
A86-410013	345	31.7	1.9	96
A86-410014	333	30.7	2.3	98
A86-410015	356	29.7	1.7	94
A86-410016	334	30.7	1.9	102
A86-410017	344	30.5	2.1	99
A86-410018	372	33.5	1.6	94
$LSD_{0.05}$[a]	22	1.3	0.2	3
$LSD_{0.05}$[b]	16	1.0	0.2	3

[a]$LSD_{0.05}$ used to compare any BC_1F_3-derived line with the recurrent parent.

[b]$LSD_{0.05}$ used to compare the donor parent with the recurrent parent.

Table I8. Mean values for four traits of the recurrent parent, donor parent, and BC_2F_2-derived lines from the Cumberland population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
Recurrent Parent				
Cumberland	344	32.4	2.0	98
Donor Parent				
Williams 82	361	34.1	1.9	105
BC_2F_2-derived Lines				
A86-407019	335	31.0	1.8	94
A86-407020	336	31.0	1.6	90
A86-407021	332	32.5	2.2	95
A86-407022	330	32.5	2.1	96
A86-407023	338	30.5	2.2	92
A86-407024	335	32.2	2.3	91
A86-407025	328	32.5	2.6	94
A86-407026	327	32.5	2.5	93
A86-407027	355	32.2	1.8	90
A86-408019	354	33.2	2.1	94
A86-408020	362	33.0	2.1	96
A86-408021	347	32.5	1.8	92
A86-408022	351	32.2	1.8	92
A86-408023	361	32.5	2.0	94
A86-408024	363	32.0	1.8	96
A86-408025	350	30.2	2.0	94
A86-408026	359	31.5	2.0	94
A86-408027	343	32.2	1.8	92

Table I8. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	$g\ m^{-2}$	days	score	cm
A86-409019	356	33.0	1.7	95
A86-409020	346	31.7	2.2	95
A86-409021	347	31.5	2.0	97
A86-409022	351	31.7	2.1	96
A86-409023	352	31.7	1.8	91
A86-409024	338	31.0	1.9	93
A86-409025	365	32.0	1.7	92
A86-409026	341	31.5	1.9	94
A86-409027	356	30.7	1.9	92
A86-410019	353	32.7	2.1	93
A86-410020	335	30.5	2.4	98
A86-410021	345	31.5	2.0	100
A86-410022	353	32.7	2.1	99
A86-410023	341	31.7	2.2	97
A86-410024	358	31.7	1.9	96
A86-410025	384	32.7	2.0	95
A86-410026	350	31.0	2.0	96
A86-410027	325	32.7	1.9	97
$LSD_{0.05}$[a]	22	1.3	0.2	3
$LSD_{0.05}$[b]	16	1.0	0.2	3

[a] $LSD_{0.05}$ used to compare any BC_2F_2-derived line with the recurrent parent.

[b] $LSD_{0.05}$ used to compare the donor with the recurrent parent.

Table I9. Mean values for four traits of the recurrent parent, donor parent, and BC_3F_2-derived lines from the Cumberland population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
Cumberland	344	32.4	2.0	98
Donor Parent				
Williams 82	361	34.1	1.9	105
BC_3F_2-derived Lines				
A86-407028	340	29.7	2.0	94
A86-407029	350	32.0	2.1	99
A86-407030	358	32.2	2.2	100
A86-407031	366	31.2	2.2	97
A86-407032	350	32.2	2.2	99
A86-407033	373	32.0	1.8	96
A86-407034	352	31.7	2.1	94
A86-407035	349	32.2	2.0	101
A86-407036	369	31.5	1.9	99
A86-408028	331	32.7	2.0	95
A86-408029	349	31.7	2.1	101
A86-408030	336	30.2	1.9	96
A86-408031	331	31.5	2.1	94
A86-408032	350	31.2	2.0	97
A86-408033	317	33.5	2.1	95
A86-408034	352	32.5	2.4	99
A86-408035	357	32.5	1.9	100
A86-408036	335	31.5	2.3	99

Table I9. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A86-409028	345	32.5	2.4	96
A86-409029	342	31.2	1.8	99
A86-409030	335	31.0	1.9	99
A86-409031	326	33.0	2.2	94
A86-409032	358	32.5	2.1	96
A86-409033	348	32.7	1.8	95
A86-409034	341	33.0	2.1	97
A86-409035	346	31.7	1.8	97
A86-409036	351	31.5	1.9	99
A86-410028	355	30.7	2.0	97
A86-410029	335	30.7	2.0	94
A86-410030	348	31.5	2.0	96
A86-410031	355	30.7	2.3	96
A86-410032	357	31.7	2.0	98
A86-410033	317	32.2	2.1	99
A86-410034	346	29.7	2.2	102
A86-410035	340	32.2	1.9	102
A86-410036	364	30.7	1.8	101
$LSD_{0.05}$[a]	22	1.3	0.2	3
$LSD_{0.05}$[b]	16	1.0	0.2	3

[a] $LSD_{0.05}$ used to compare any BC_3F_2-derived line with the recurrent parent.

[b] $LSD_{0.05}$ used to compare the donor parent with the recurrent parent.

Table I10. Mean values for four traits of the recurrent parent, donor parent, and BC_4F_2-derived lines from the Cumberland population combined across three environments

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
Recurrent Parent				
Cumberland	344	32.4	2.0	98
Donor Parent				
Williams 82	361	34.1	1.9	105
BC_4F_2-derived Lines				
A86-407037	345	29.2	1.9	93
A86-407038	374	31.5	1.9	93
A86-407039	361	31.2	1.8	95
A86-407040	343	28.2	1.7	96
A86-407041	345	29.2	1.8	99
A86-407042	338	31.2	1.8	96
A86-407043	336	31.7	2.3	99
A86-407044	355	31.2	2.1	100
A86-407045	336	30.7	2.2	99
A86-408037	342	32.0	2.3	101
A86-408038	359	30.7	2.5	97
A86-408039	365	29.2	2.1	97
A86-408040	365	31.5	2.2	98
A86-408041	376	32.2	2.0	96
A86-408042	356	30.5	1.9	97
A86-408043	371	33.5	2.0	100
A86-408044	344	30.7	1.9	94
A86-408045	348	32.2	2.0	96

Table I10. (continued)

Entry Designation	Trait			
	Yield	Maturity	Lodging	Height
	g m^{-2}	days	score	cm
A86-409037	356	30.2	1.8	95
A86-409038	355	31.2	1.8	100
A86-409039	348	31.0	1.9	102
A86-409040	324	31.7	1.9	99
A86-409041	355	31.2	2.0	98
A86-409042	348	31.7	2.0	96
A86-409043	356	32.7	1.9	97
A86-409044	319	32.2	2.1	97
A86-409045	334	31.5	2.2	98
A86-410037	357	30.7	2.3	102
A86-410038	362	30.2	1.9	92
A86-410039	344	28.5	1.8	98
A86-410040	344	31.7	2.3	97
A86-410041	354	30.5	2.1	92
A86-410042	353	31.0	2.1	99
A86-410043	341	30.5	2.5	100
A86-410044	376	31.7	1.8	100
A86-410045	360	30.5	1.9	97
$LSD_{0.05}$[a]	22	1.3	0.2	3
$LSD_{0.05}$[b]	16	1.0	0.2	3

[a] $LSD_{0.05}$ used to compare any BC_4F_2-derived line with the recurrent parent.

[b] $LSD_{0.05}$ used to compare the donor parent with the recurrent parent.

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